

**FACTORS AFFECTING MOVEMENT PATTERNS OF MULE DEER (*ODOCOILEUS*
HEMIONUS) IN SOUTHERN SASKATCHEWAN: IMPLICATIONS FOR CHRONIC
WASTING DISEASE SPREAD**

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By

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ABSTRACT

Chronic wasting disease (CWD) has been a known threat to Saskatchewan's wild cervid populations for more than a decade. As host movements can affect the spread of a disease across the landscape, disease models and management strategies should incorporate information regarding movement patterns of the host population in question. I used radio telemetry to study mule deer (*Odocoileus hemionus*) captured between 2006 and 2008 in a CWD-endemic region of southern Saskatchewan. Using location data from 152 individuals, I investigated home range size and patterns of direct and indirect contact (measured using proximity and shared space use) in relation to sex, habitat, and landscape structure.

Home ranges (95% fixed kernel) of GPS-collared deer in this study averaged 21.4 km² (n = 94). Male home ranges (\bar{x} = 29.5 km², n = 56) were larger than those of females (\bar{x} = 16.1 km², n = 38), which could have implications for CWD prevalence differences between sexes. Of the landscape variables tested, topographic ruggedness was inversely related to home range size and Shannon's diversity (a measure of both habitat richness and evenness) was positively related to home range size.

Potential direct contact events were identified when two deer were located within 25 m of each other at the same point in time. These events occurred more often between February and April, agreeing with the tendency of mule deer to aggregate into large groups during the late winter months, and suggesting that this may be an important time period for disease transmission. Contact also occurred more than expected in cropland, whereas areas of shared use occurred more than expected in grassland, shrub/wood habitat, and rugged terrain. Smaller home ranges and greater degree of shared space use within areas of rough topography may lead to

greater risk of environmental contamination with the infectious CWD agent in these areas. In contrast, the relationship between cropland and probability of direct contact may imply greater risk of direct CWD transmission between deer occupying this habitat.

These results identify connections between particular landscape factors and risk of CWD transmission and will be used, in combination with results of related studies, to develop a model of CWD spread in Saskatchewan. This will in turn aid management agencies in developing methods to more effectively manage the disease and control its movement outside of affected regions.

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LIST OF ABBREVIATIONS

AIC	Akaike Information Criteria
ANOVA	Analysis of Variance
CCWHC	Canadian Cooperative Wildlife Health Centre
CWD	Chronic Wasting Disease
GIS	Geographic Information System
GPS	Global Positioning System
h_{ref}	Reference bandwidth
HRT	Home Range Tool
LMT	Local Mean Time
LSCV	Least Squares Cross Validation
MCP	Minimum Convex Polygon
SPOT	Satellite Pour l'Observation de la Terre
TSE	Transmissible Spongiform Encephalopathy
UD	Utilization Distribution
UHF	Ultra High Frequency
VHF	Very High Frequency

CHAPTER 1 INTRODUCTION AND LITERATURE REVIEW

1.1 Chronic Wasting Disease

1.1.1 Introduction to chronic wasting disease

Chronic wasting disease (CWD) is a transmissible spongiform encephalopathy (TSE) (Williams, Young 1980) that affects farmed and wild cervid populations in North America. Since its discovery in the 1960s in captive mule deer (*Odocoileus hemionus*) facilities in Colorado, this disease has become the focus of research for many wildlife agencies and institutions. CWD is caused by misfolded proteins called prions (Prusiner 1982) that are infectious and highly resistant to degradation. These infectious particles accumulate in nervous and lymphoid tissue and cause degenerative changes in the brain, eventually leading to death. Infected individuals can transmit CWD to others through direct physical contact, but also by shedding prions into the environment, where they may remain infective for years (Miller et al. 2004, Johnson et al. 2006, Tamguney et al. 2009).

Because of the potential for transmission through environmental contamination, CWD has presented great challenges in all attempts at eradication or stopping its spread. Although a great deal of information has been uncovered in the past three decades regarding the cause of CWD and its impact on infected individuals, many aspects of transmission and population level effects remain unknown. Models have predicted major population declines (Gross, Miller 2001) and although these predictions have been widely debated (Schauber, Woolf 2003), researchers have begun to see evidence of adverse population-level effects in areas of high CWD prevalence

(Miller et al. 2008). Even without directly causing population declines, CWD may harm cervid populations by altering demographics and amplifying the effects of other diseases or stressors. The disease could also affect recreational hunting due to demographic changes and public concerns about contaminated meat (Needham et al. 2004). To date, CWD has been found in free-ranging and captive white-tailed deer (*O. virginianus*), mule deer, and elk (*Cervus elaphus*), and more recently in free ranging moose (*Alces alces*) (Baeten et al. 2007).

1.1.2 History of CWD in Saskatchewan and North America

In 1967, an unidentified neurological disease was recognized among mule deer in a captive research facility in Colorado (Williams, Young 1980). The disease persisted in this facility and was identified by researchers during later years as a spongiform encephalopathy and eventually described as chronic wasting disease (Williams, Young 1980). CWD was also recognized in a Wyoming research facility during the late seventies. The discovery of CWD in wild elk in Colorado in 1981 and shortly afterward in Wyoming set this disease apart from other transmissible spongiform encephalopathies (TSEs) as the only one that affects free ranging species (Spraker et al. 1997, Williams, Miller 2002, Williams et al. 2002a). Surveillance over the next two decades uncovered infected white-tailed and mule deer in both Wyoming and Colorado, and later in Nebraska, which led to the designation of an endemic focus, covering areas of southeast Wyoming, northeast Colorado, and southwest Nebraska (Williams, Miller 2002).

In 1996, CWD was detected in a farmed elk in Saskatchewan, which prompted the initiation of surveillance programs in the province for both farmed and wild cervids during the following year. Surveillance efforts were intensified and a herd reduction program implemented after the 2000 detection of CWD in a wild mule deer south of Lloydminster in west-central Saskatchewan. The herd reduction program involved increasing hunting opportunities in areas

around the initial detection in order to reduce deer densities. This included distributing antlerless tags at no cost, earn-a-buck incentives, and removing limits in these areas in return for hunters submitting the heads of harvested deer for testing.

During the following years, this program resulted in the detection of new foci in Saskatchewan, as well as the designation of two areas where the disease is considered to be well established: the Saskatchewan Landing area and another area further north near Nipawin. Both areas are thought to have been initially infected by separate spillover events from infected game farms (Bollinger et al. 2004). CWD has since been found in several other areas around Saskatchewan, including wildlife management zones just south of Saskatoon and near the Alberta border (Figure 1.1). In Saskatchewan, prevalence in wild mule deer and white-tailed deer populations is currently low, ranging between 0.5% and 2.6% in affected regions (Canadian Cooperative Wildlife Health Centre, *unpublished data*), but researchers in areas of Colorado have documented prevalence increases to as high as 25% (Miller et al. 2008). In 2005, the disease was detected in a free-ranging mule deer in Alberta, which prompted the Alberta government to implement similar herd reduction programs to try and eradicate the disease within the province and prevent further spread across the Saskatchewan-Alberta border. CWD is currently known to occur in wild cervid populations of 13 states and two provinces and continues to affect the North American farmed cervid industry.

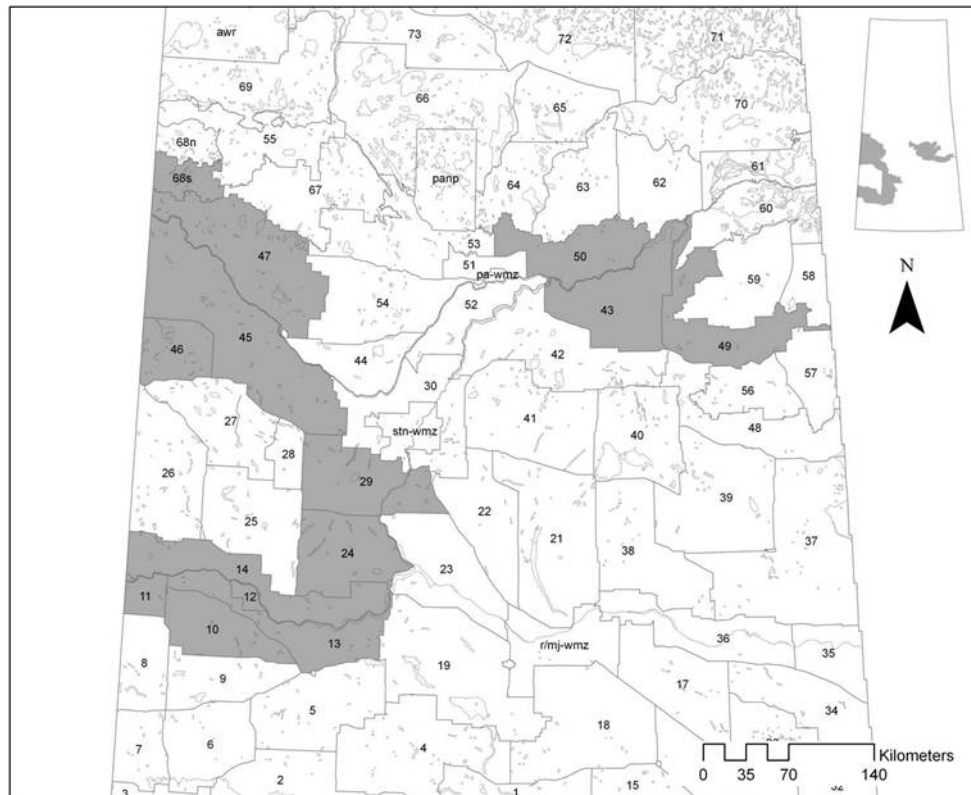


Figure 1.1. Wildlife Management Zones in Saskatchewan with CWD positive wild deer and/or elk as of March, 2009 (Saskatchewan Ministry of Environment 2009).

1.1.3 Management Challenges

So far no state or province has been successful in eradicating chronic wasting disease once it has been detected in wild populations, despite varying degrees of effort and methods of management. Reasons for this are many, but a primary issue is the lack of understanding regarding transmission pathways of CWD. Although advances have been made over the past three decades, there is still disagreement among researchers whether transmission of CWD occurs in a frequency-dependent manner, where transmission rates are independent of population density, or a density-dependent manner, where transmission will decline with reduced population density (Wasserberg et al. 2009). This is further confounded by the uncertainty surrounding

environmental transmission (Miller et al. 2004). The length of time that prions remain infectious in the environment is thought to be many years, but duration and degree of infectivity may be influenced by environmental factors such as soil composition (Johnson et al. 2006, Schramm et al. 2006). Until methods are developed to detect prions and reduce infectivity in the environment, herd reduction will be ineffective unless population densities in affected areas can be kept at extremely low levels for extended periods of time (Gross, Miller 2001).

Drastic measures such as herd reduction cause many political and financial issues, and public support is difficult to maintain, particularly over the long term. In order for CWD management programs to be successful, cooperation is required between government agencies, researchers, the farmed cervid industry, hunters, landowners, and the general public. This relationship is complicated not only by conflicting interests, but also by the incomplete knowledge upon which management strategies must be based. In addition, even if programs are successful, there is expected to be a lag in measureable prevalence changes of up to 11 years (Wasserberg et al. 2009), which could have major implications for funding and support. Researchers and management officials now recognize that once CWD becomes established in an area, eradication of the disease is unlikely given the management options that are currently available (Pybus, Hwang 2008, Williams et al. 2002b, Miller et al. 2006). This has led to a shift in management focus towards preventing and controlling spread of CWD into previously unaffected areas (Williams et al. 2002b, Pybus, Hwang 2008).

1.2 Importance of animal movement

Understanding the spread of a disease requires an understanding of host populations and how they distribute themselves across the landscape. Hosts of chronic wasting disease are highly mobile, gregarious animals that occupy home ranges and associate with each other in a non-

random manner. Movements are driven by a mix of biological and ecological factors, which individuals respond to in their attempts to meet nutritional needs, avoid predation, and successfully produce offspring (Gautestad, Mysterud 1993). These individual movements can in turn affect larger-scale processes like disease dynamics (Patterson et al. 2008). High contact rates between individuals, long distance movements such as dispersal and migration, and large home range sizes have all been identified as aspects of deer movement that may contribute to disease spread (Conner, Miller 2004, Schaubert et al. 2007, Kjær et al. 2008, Skuldt et al. 2008). These factors are not generally considered in the designation of disease management zones, which are often based on man-made boundaries such as counties, rural municipalities or readily identifiable features such as roads that provide no natural barriers to animal movement. The same can be said for many disease models and measures of prevalence, which are often calculated at scales that cannot account for animal movement or heterogeneities in disease spread (Conner, Miller 2004).

Deer movement and chronic wasting disease has been studied in several areas affected by the disease (Conner, Miller 2004, Kjær et al. 2008, Skuldt et al. 2008, Long et al. 2005, Farnsworth et al. 2006), but geographic and species differences in movement patterns suggest a need for region-specific studies to be conducted. If we gain an understanding of how deer movements are influenced by the surrounding landscape in specific areas affected by CWD, we can not only apply this information to models predicting disease spread, but also identify commonalities with longer-affected regions and learn from their experiences in developing effective management strategies.

1.3 Thesis summary

1.3.1 Objective

The overall objective of this study is to identify environmental and biological factors influencing movement patterns and social behaviour of mule deer in southern Saskatchewan and how these factors may affect CWD transmission and spread.

1.3.2 Thesis topics

1. Determine how habitat and landscape structure influence home range sizes of male and female mule deer in our study areas.
2. Quantify seasonal and sex-based differences in contact rates between GPS-collared mule deer, as well as habitat and landscape factors that may be associated with increased contact probability (both direct and indirect) and potential CWD transmission in southern Saskatchewan.

1.3.3 Rationale

Knowledge gained through this study may be used as a valuable tool in developing a predictive spatial model of chronic wasting disease spread in Saskatchewan. Models such as these will allow management agencies to focus their efforts in areas of high risk for CWD introduction and develop methods to more effectively reduce prevalence in affected areas and control the spread of CWD outside of these regions.

CHAPTER 2 OVERALL METHODS

2.1 Study species: Mule deer (*Odocoileus hemionus*)

Mule deer are an important large herbivore found in Saskatchewan, where they overlap with other cervids such as white-tailed deer (*O. virginianus*), elk (*Cervus elaphus*), and moose (*Alces alces*) in some portions of the province. The species, which includes both black-tailed and mule deer, belongs to the taxonomic family Cervidae, within the order Artiodactyla. The entire species range stretches across western and central North America, as far north as Alaska and Yukon Territory and as far south as Mexico, with each of ten recognized subspecies occupying a different portion of the range (Figure 2.1) (Anderson, Wallmo 1984, Mackie 1994). Of these subspecies, the Rocky Mountain mule deer (*O. h. hemionus*) spans the largest area and is the only one found in Saskatchewan (Mackie 1994, Anderson, Wallmo 1984, Kie, Czech 2000). Mule deer coexist with white-tailed deer in many parts of their range, and although the two species may occasionally produce hybrid offspring (Wishart 1980), they are thought to be generally segregated by differences in preferred habitat (Lingle 2002, Martinka 1968, Swenson et al. 1983, Wood et al. 1989) and predator avoidance strategies (Lingle 2002, Martinka 1968, Swenson et al. 1983, Wood et al. 1989). In 2006, the overall population of mule deer in Saskatchewan was estimated at around 43,000 individuals, with the majority occurring in the south-west corner of the province (Saskatchewan Ministry of Environment 2008b).

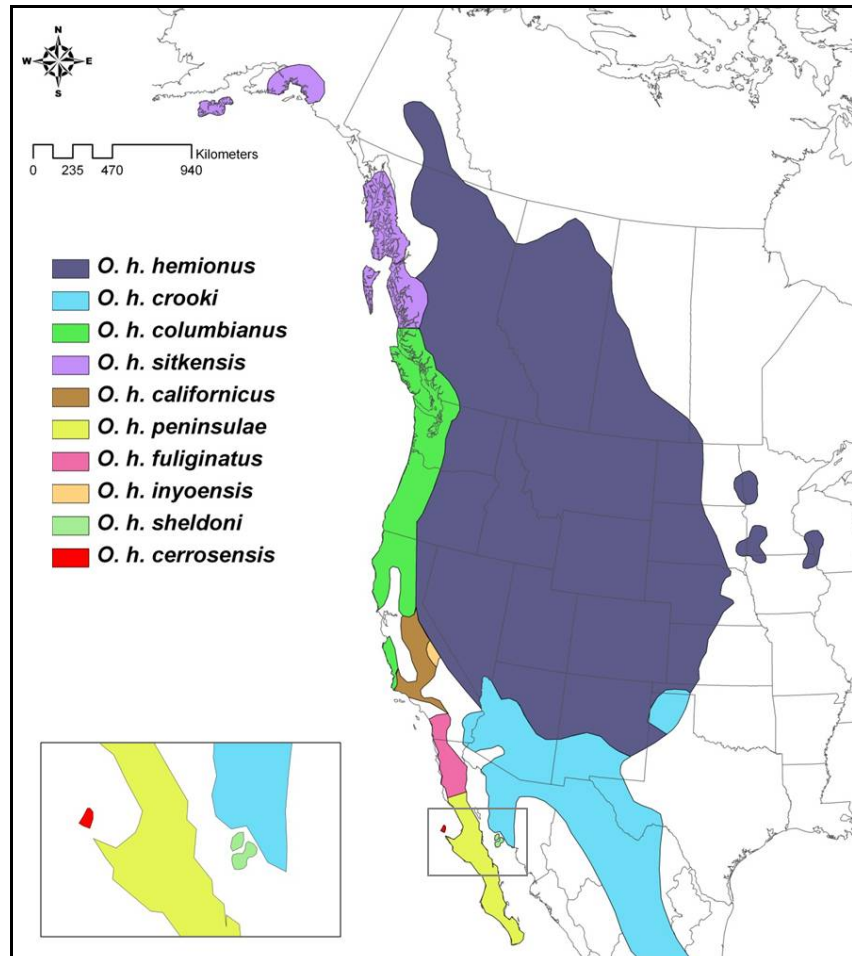


Figure 2.1. Distribution of mule deer and recognized subspecies in North America (Mackie 1994).

Mule deer are highly valued in Saskatchewan for a number of reasons. As large herbivores, they play a major role in nutrient cycling, plant succession, and other processes that are crucial in the maintenance of healthy ecosystems (Hobbs 1996). They also provide an important food source for predators like coyotes (*Canis latrans*) and cougars (*Puma concolor*) and scavengers such as raccoons (*Procyon lotor*), crows (*Corvus brachyrhynchos*) and turkey vultures (*Cathartes aura*) (Jennelle et al. 2009). Although frequently involved in human-wildlife

conflict through highway collisions and crop damage, mule deer are particularly important to humans for their aesthetic significance as well as their economic value as a game species.

Hunting is of great cultural and economic importance to Saskatchewan. The annual gross expenditures related to hunting (all game species) in the province amount to over 107 million dollars (Murray 2006). Although white-tailed deer are the most commonly hunted big game species in the province, mule deer made up about 17% of cervid licenses sold in the province in 2007 (Saskatchewan Ministry of Environment 2008a).

Mule deer occupy a variety of habitat types throughout their range, but are well adapted to the open prairie and are common in grasslands of southern Saskatchewan, tending to prefer areas of rugged or rolling topography (Wood et al. 1989, Lingle 2003). Many are seasonally migratory, travelling short or long distances to seek out suitable fawning areas, food resources, or protection from harsh winter elements (Nicholson et al. 1997, Brown 1992, Garrott et al. 1987). Researchers report varying percentages of migratory mule deer within study populations (Conner, Miller 2004, Wood et al. 1989, Sawyer et al. 2005) with some groups of monitored deer reported as entirely migratory (Garrott et al. 1987) and others as entirely non-migratory (Eberhardt et al. 1984). In mountainous regions, migrations are often between a high elevation summer range and a lower elevation winter range (Conner, Miller 2004, Garrott et al. 1987, Sawyer et al. 2005, D'Eon, Serrouya 2005). Distance between seasonal ranges has been reported as high as 158 km (\bar{x} = 84.1 km) for GPS-collared mule deer in western Wyoming, where researchers found 95% of collared deer to be migratory (Sawyer et al. 2005). Migration distances were shorter in a study of mule deer inhabiting a prairie region of eastern Montana, with a maximum distance of 80 km and an average distance of 5.9 km between summer and winter ranges (Wood et al. 1989).

Patterns of sociality are also influenced by season. Females are reported to isolate themselves in late spring to deliver and tend to their fawns (Wood et al. 1989). This contrasts with large groups of mixed sex and age classes often seen in late winter (Conner, Miller 2004, Wood et al. 1989, Lingle 2003). Aggregatory behaviour during the late winter could be due to the need to procure scarce food resources (Wood et al. 1989) combined with the added protection of a large group (Bowyer et al. 2001), which may be necessary where travel is hindered by snow. In our study areas, breeding season peaks between late November and early December, but timing may be variable for different geographic regions throughout the mule deer range (Kie, Czech 2000). Their breeding strategy is considered to be polygynous, in which males will attempt to breed with multiple females, tending to each until breeding occurs (Geist 1981).

Although there is a moderate amount of literature available on home range sizes of mule deer, reports of home range sizes are difficult to compare due to the wide variety of methods used in calculations of home range as well as the duration of time for which the home range is reported. In general, male mule deer are reported to have larger home ranges than female mule deer (Robinette 1966, Relyea et al. 2000), although this relationship has not been found to be significant in all cases (Eberhardt et al. 1984). Home ranges vary widely among studies, and researchers have reported average mule deer year-round home range sizes ranging from 0.49 km² (*O. h. fuliginatus* in southern California, 95% adaptive kernel home range, n = 2) (Kie et al. 2002) to 39.8 km² (*O. h. hemionus* in south central Washington, 95% confidence ellipse home range, n = 34) (Eberhardt et al. 1984).

Much of the available literature on mule deer movement is derived from studies undertaken in mountainous areas of the US (Conner, Miller 2004, Relyea et al. 2000, Kie et al. 2002, Kufeld et al. 1988b). Information is lacking for mule deer in prairie-dominated regions

with the exception of a few studies (Lingle 2002, Swenson et al. 1983, Wood et al. 1989, Lingle 2003, Wood 1989), and variation in home range sizes and movement patterns from other geographic regions suggests that much of this information may not be applicable across all populations of mule deer.

Movements and behaviour of mule deer also differ from those of white-tailed deer. Examples of these differences can be seen in their habitat use as well as in their response to predators (Lingle 2002, Martinka 1968, Swenson et al. 1983, Wood et al. 1989). A study of sympatric mule deer and white-tailed deer populations in a prairie-dominated area of Alberta found that white-tailed deer tend to move onto gentler terrain in response to predators (Lingle 2002). In contrast, mule deer are more likely to move onto rugged terrain where their specialized stotting gait gives them an advantage over predators (Lingle 2002). Mule deer are also more likely to remain in groups and defend themselves against predators such as coyotes, while white-tailed deer prefer to flee in response to threat (Lingle 2003). In general, it has been shown that rugged terrain is a key component to mule deer habitat and that agricultural land and wooded riparian habitats are more important for white-tailed deer (Swenson et al. 1983, Wood et al. 1989). In Montana, researchers found that home ranges of white-tailed deer were larger ($\bar{x} = 33.5 \text{ km}^2$) and less discrete than those of mule deer ($\bar{x} = 13.85 \text{ km}^2$) in the same area due to greater movement within the home range in general, and more activity shifts in response to resource availability (Wood et al. 1989). In contrast, researchers in Wisconsin report sedentary, non-migratory populations of white-tailed deer, occupying home ranges of less than two square kilometers (Skuldt et al. 2008). Harestad and Bunnell (1979) also found that white-tailed deer generally have smaller home ranges than mule deer, based on a number of studies. Movement patterns of both species vary widely from one geographic region to the next, but differences

between those of mule deer and white-tailed deer within similar environments suggest that the two species should be considered separately for management purposes.

2.2 Study areas

This study was conducted in five sites in rural southern Saskatchewan near the Lake Diefenbaker area of the South Saskatchewan River (Bounded by $-108^{\circ}27'21''$ and $51^{\circ}9'46''$ in the northwest and $-106^{\circ}12'28''$, $50^{\circ}24'40''$ in the southeast) (Figure 2.2). Of the five study areas, Antelope creek (Antelope), Swift Current Creek (Swift), and the Beechy and Matador community pastures (Beechy and Matador) are within CWD management zones but the most north-easterly site, Douglas Provincial Park (Douglas), is just outside. At the start of the research project, the Beechy site was also located outside of the management zones, but the zones have since been expanded. Douglas falls within the Moist Mixed Grassland Ecoregion of Saskatchewan, while the other four are found in the Mixed Grassland Ecoregion (Acton et al. 1998). The Mixed Grassland Ecoregion is characterized by a semiarid climate with mean annual precipitation of 352 mm, mean July temperature of 18.9°C and mean January temperature of -12.6°C (Acton et al. 1998). The total area covered by all study sites combined is equal to approximately 2700 km^2 , with each site ranging from approximately 250 to 800 km^2 .

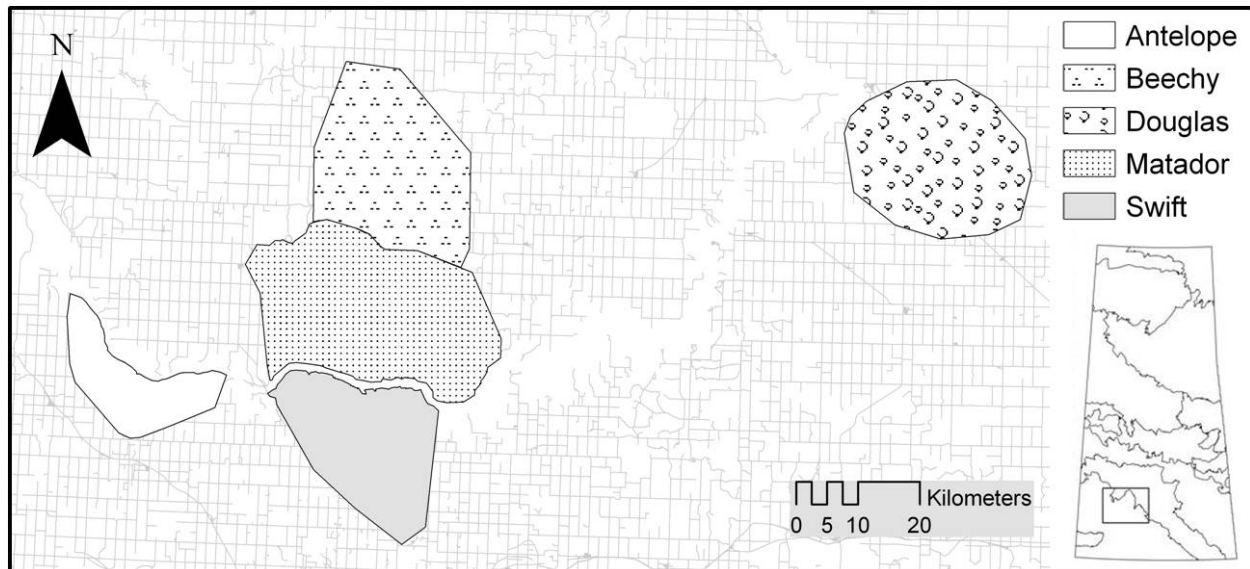


Figure 2.2. Locations of study sites in southern Saskatchewan.

Annual cropland makes up a major proportion of the study sites, while other common habitat types are mixed grass prairie across rolling pastureland and through the river valley interspersed with wetlands and patches of low shrub in coulees and draws (Acton et al. 1998). Grasslands in this region are composed mostly of wheatgrass (*Agropyron spp.*), needle-and-thread speargrass (*Stipa comata.*), blue grama grass (*Bouteloua gracilis*), and june grass (*Koeleria macrantha*). Pasture sage (*Artemisia frigida*) and moss phlox (*Phlox hoodii*) are examples of forbs found among the grass species, and snowberry (*Symphoricarpos occidentalis*) and wolf willow (*Eleagnus commutata*) are common shrubs. Annual crops grown in these study areas are barley, durum, wheat, oats, canola, peas and lentils (Saskatchewan Ministry of Agriculture 2008). Perennial forage crops such as alfalfa are grown in these areas as well. Very little forest cover is present in all areas except Douglas, where patches of aspen forest (*Populus tremuloides*) are dispersed among pastureland and sand hills dominated by creeping juniper (*Juniperus horizontalis*), chokecherry (*Prunus virginiana*), and rose (*Rosa acicularis*).

Antelope and Swift are located on the south side of the South Saskatchewan River, to the west and east of Saskatchewan Landing Provincial Park, respectively. These sites are similar in that they are composed of one or a series of creek valleys running perpendicular to the main river valley. The terrain is generally more rugged than that of the other sites, particularly in Swift, where the large creek valley containing numerous hills and coulees is bordered by steep cliffs, separating it from the surrounding cropland. Similarly to those in Antelope, where several creek valleys create a network of coulees, ravines and draws, these rugged topographic features provide distinct areas of suitable mule deer habitat surrounded by developed agricultural land.

In contrast, the Beechy and Matador study areas found north of the South Saskatchewan River are the largest sites, composed of a large, relatively continuous expanse of rolling community pasture. Matador meets the river to the south, where the rugged river valley creates a landscape similar to that of Antelope and Swift, but transforms into a plateau of grassland and crop that climbs in elevation and becomes progressively hillier to the north. Beechy and Matador are separated only by a secondary highway which provides no significant barrier to deer movement between the sites. Rolling hills continue north throughout the Beechy site, where grassland, seasonal wetlands, and patches of low-lying shrub form a favorable landscape for mule deer. Road density is very low in Beechy and Matador, particularly during the winter months when trails become inaccessible, which minimizes human disturbance for deer and other wildlife inhabiting these study areas.

2.3 Field methods

2.3.1 Deer capture and collaring

Deer were captured between January and April of 2006, 2007 and 2008 using either clover traps (Clover 1956) (2007 and 2008) or a helicopter and net-gun (Barrett et al. 1982)

(2006 and 2007). Clover traps were modified following McCullough (1975), and trap height was increased to 50" to facilitate capture of large adult bucks. All deer were chemically immobilized with intramuscular injections of Telazol® and Xylazine (Rompun®) combined. We collected tonsil samples for chronic wasting disease testing, blood and feces for studies of other diseases and parasites, and ear tissue for genetic research. Weight and body measurements were taken for body condition evaluation and age of each deer was estimated by assessing tooth wear. Each deer was fitted with a VHF (Very High Frequency) collar (LOTEK, ATS) or GPS (Global Positioning System) collar (LOTEK, Televilt) and reversed with Atipamezole (Antisedan®) after collar deployment and sample collection. For males, collars were fitted with a specially designed foam insert to allow for neck expansion during the rut. Animal handling protocol was approved by the Animal Care and Use Committee (Permit # 20050135).

2.3.2 Radio telemetry

The majority of GPS collars were programmed to automatically take fixes every 1-4 hours, with more frequent fixes occurring during key periods like fawning and breeding seasons. GPS collars manufactured by Televilt were programmed for less frequent fixes (every 8 hours) but relatively few collars of this type were deployed (4 of 94). In order to avoid bias due to higher sampling frequency during particular seasons, location data collected at intervals shorter than 4 hours were removed from all analyses. Fix times for all remaining data were 4:00, 8:00, 12:00, 16:00, 20:00, and 24:00 local mean time (LMT). A portion of the collars were equipped with UHF (Ultra High Frequency) remote-downloading capabilities whereas others stored all GPS data on board for the duration of deployment. All VHF-collared deer were located at least once a month by small aircraft or on foot. GPS collars were also tracked, though less precisely, to identify long distance movements and to periodically download data from UHF-equipped

collars. Upon identification of a mortality signal, the carcass was located as quickly as possible to determine cause of death and to retrieve the collar. Final collar retrieval for the project occurred during February and March of 2009. Deer in the Antelope Creek study area were re-collared at that time for additional research.

GPS collars were reported by LOTEK to be accurate within 5 m. Additional accuracy testing was performed by allowing collars ($n = 4$) to collect location information from fixed positions and calculating the distance between each location and the center point of all locations. This resulted in an average error of 11.3 m, with individual collar error ranging from 6.1 m (SD = 5.1 m, $n = 63$ locations) to 18.4 m (SD = 44.7 m, $n = 116$ locations). Average fix success for all collars used in the study was 95.7% (Range: 46.3 – 100%) and average proportion of 3D locations was 97.0% (Range: 81.8 – 100%). Aerial tracking accuracy for VHF collars was tested by comparing locations estimated through aerial tracking of mortality events to actual locations collected from the ground. Using this method, average error for VHF data was 678 m ($n = 82$ locations, SD = 432 m).

Coordinates with zero values were removed from GPS collar datasets, as well as obvious errors such as points located in different parts of the world or locations associated with negative altitude values. To identify additional suspect data points within GPS collar data, each individual's dataset was examined visually. Outliers were identified and assessed based on average movement distances and patterns of movement leading up to and following the points in question to determine whether they were due to long distance movements or caused by collar error.

2.4 Data processing

2.4.1 Landscape classification

A classified land cover map was created for the five study areas using 20 m resolution, multispectral SPOT (Satellite Pour l'Observation de la Terre) images obtained during July and September of 2007 (Alberta Terrestrial Imaging Centre 2007). Raw images were orthorectified using PCI Geomatica software (PCI Geomatics 2005) and were not radiometrically processed. Images covering the Swift, Matador, Beechy and Antelope study sites were collected within the same time period (July 2007), which allowed us to mosaic the images and classify them together. Collection of one image relevant to the Douglas study area was delayed until September 2007, so this image was classified separately due to spectral differences.

Vegetation training data were collected along transects in each study area throughout the summer of 2007 in conjunction with a deer population survey. Each location of field data collection was overlaid with SPOT imagery and the associated pixel or pixels were classified as the land cover type documented at that location. Additional training sites were identified and classified through visual interpretation of the 20 m SPOT imagery and high resolution (2.5 m) panchromatic SPOT imagery (Telus 2006), guided by knowledge of the area obtained during field activities. Only locations that could be classified with a high level of certainty were used as supplementary training sites. Thirty percent of all training or “ground truth” polygons were withheld as reference data for accuracy assessment, while the remaining 70% were used as training locations for the classification process.

Digital elevation model (Government of Canada, Centre for Topographic Information 2000-2009) and terrain ruggedness layers (Evans 2004) (both 25 m resolution) were used to supplement remotely sensed imagery and add a topographic dimension to the classification (See

section 2.4.2 for details). These layers were stacked with the SPOT images, along with an additional layer created by applying a homogeneity filter to the SPOT near infrared band. Pixel size was resampled to 25 m and supervised classification was performed within ENVI software (ITT Visual Information Solutions 2008) using a maximum likelihood classifier. Resolution of the final product was 25 m.

The original classification scheme consisted of nine classes: crop, grassland, mixed grass/shrub, shrub, woodland, wetland, open water, unvegetated, and unclassified; however, due to difficulties distinguishing between certain classes, the image was reclassified using only five classes (Figure 2.3). As the mixed grass/shrub class was created to represent low lying shrub habitats dominated by grasses, this class was combined with the grassland class. The shrub and woodland classes were combined because of the relative lack of woodland throughout all areas except Douglas, and the resulting lack of woodland training locations. Annual cropland and perennial forage cropland were classified together and combined with the unvegetated class because the vast majority of unvegetated areas were associated with unplanted or cut cropland. Open water and wetland classes were combined as well. The final, broad classification scheme was accepted for the purposes of this study due to its biological relevance to mule deer behaviour.

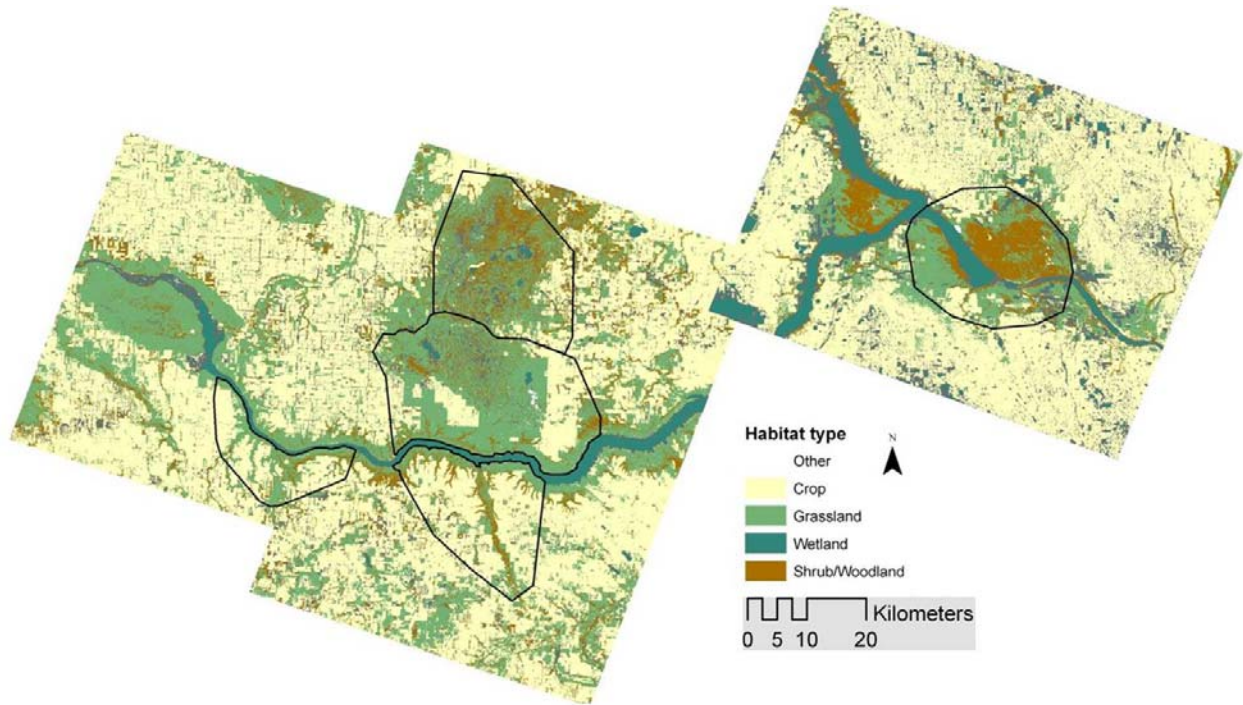


Figure 2.3. Classified land cover map of study sites and surrounding areas.

Overall accuracy of the Douglas map was 90.4% (Table 2.1b) while the accuracy of the map covering the remaining sites was 91.3% (Table 2.1a). These numbers are to be viewed with caution, however, as they are inflated by a disproportionate amount of training data collected in crop and grassland, the classes with the highest accuracy. Also, because the majority of training and reference data were collected within the five study sites, the accuracy outside of these areas may vary.

Table 2.1. Error matrices for classified maps covering the Antelope, Beechy, Matador and Swift study areas (a) and the Douglas study area (b). All data are expressed in number of pixels unless otherwise indicated.

a.		Reference data						
		Crop	Grassland	Shrub/woodland	Wetland	total	Commission error	User accuracy (%)
Classified Map	Crop	1349	1	0	2	1352	3	99.8
	Grassland	0	1676	20	5	1701	25	98.5
	Shrub/woodland	11	27	30	44	112	82	26.8
	Wetland	0	16	4	22	42	20	52.4
	Total	1360	1720	54	73	3207	130	91.3
Omission error		11	44	24	51	130		
Producer accuracy (%)		99.2	97.4	55.6	30.1	91.3		
b.		Reference data						
		Crop	Grassland	Shrub/woodland	Wetland	total	Commission error	User accuracy (%)
Classified Map	Crop	1707	2	0	0	1709	2	99.9
	Grassland	31	119	3	0	153	34	77.8
	Shrub/woodland	42	89	284	34	449	165	63.3
	Wetland	457	48	8	4820	5333	513	90.4
	Total	2237	258	295	4854	7644	714	90.4
Omission error		530	139	11	34	714		
Producer accuracy (%)		76.3	46.1	96.3	99.3	90.4		

2.4.2 Terrain Ruggedness Index (TRI) calculation

Terrain ruggedness was calculated for areas in and around the study sites using a Topographic ruggedness script (Evans 2004) for ArcGIS (ESRI 2007) and 25 m resolution digital elevation model (DEM) data (Government of Canada, Centre for Topographic Information 2000). The DEM data was produced using 1:50,000 tiles of National Topographic Database source data (1999), accurate horizontally within the circular map accuracy standard of 25 m and vertically within the 10 m linear map accuracy standard of the Centre for Topographic

Information. The topographic ruggedness script builds on methods developed by Riley et al. (1999) where a terrain ruggedness index (TRI) value is calculated for each cell by averaging the differences in elevation between that cell and its surrounding cells. Using a DEM raster as input, the topographic ruggedness script creates a new raster representing elevational change in meters, in which high values indicate rugged topography and low values indicate flat topography (Figure 2.4).

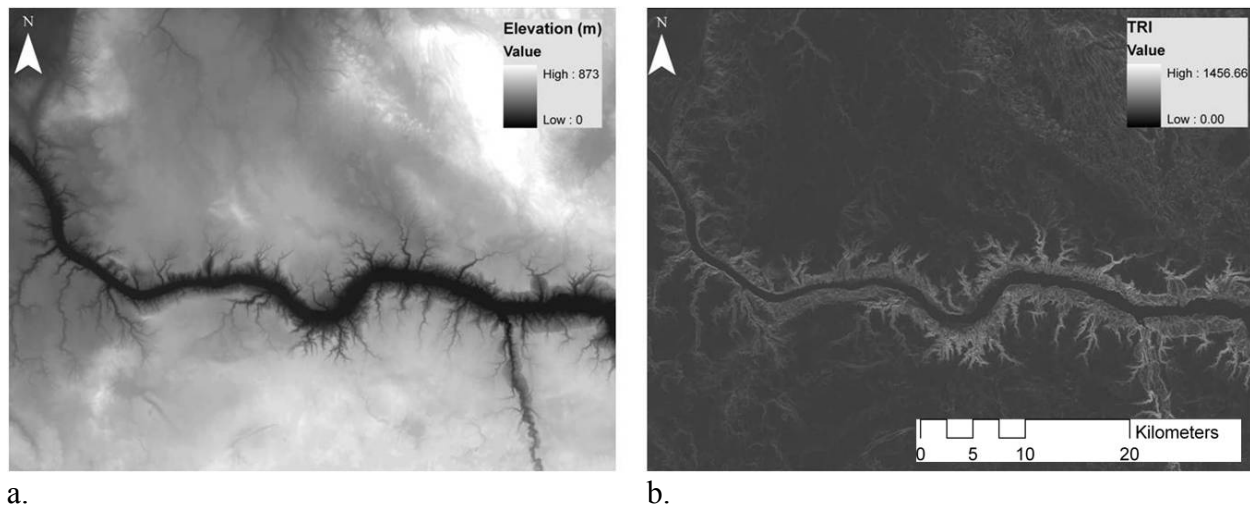


Figure 2.4. Conversion of a digital elevation model (a) to a terrain ruggedness index (TRI) (b).

2.4.3 Home range calculation

Fixed kernel home ranges were calculated for each deer using the Home Range Tools (HRT) (Rodgers et al. 2007) extension for ArcGIS (ESRI 2007). This extension uses a bivariate normal kernel estimation to build a raster of probability values based on the utilization distribution (UD) of all locations for an individual (Figure 2.5b), with each cell value representing the likelihood that an individual may be located in that particular cell over a period

of time (Kernohan et al. 2001). Unlike minimum convex polygons (MCP), kernels allow for the exclusion of brief excursions and distinction between migratory home ranges (Figure 2.6). Grid resolution was set at 50 meters and contours delineating 95% of the estimated UD volume for each individual were used in the calculation of home range size (Figure 2.5c).

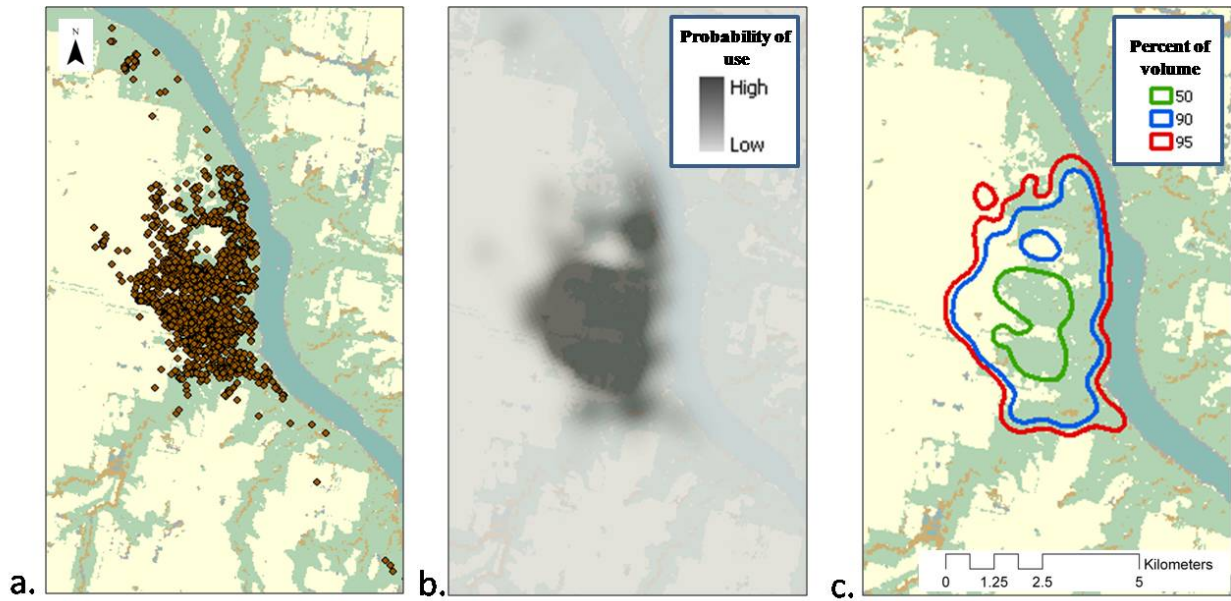


Figure 2.5. Calculation of a fixed kernel home range. GPS locations taken at four-hour intervals (a) are used to calculate a raster representing probability of use (b), from which volume contours are generated to be used in home range analysis (c).

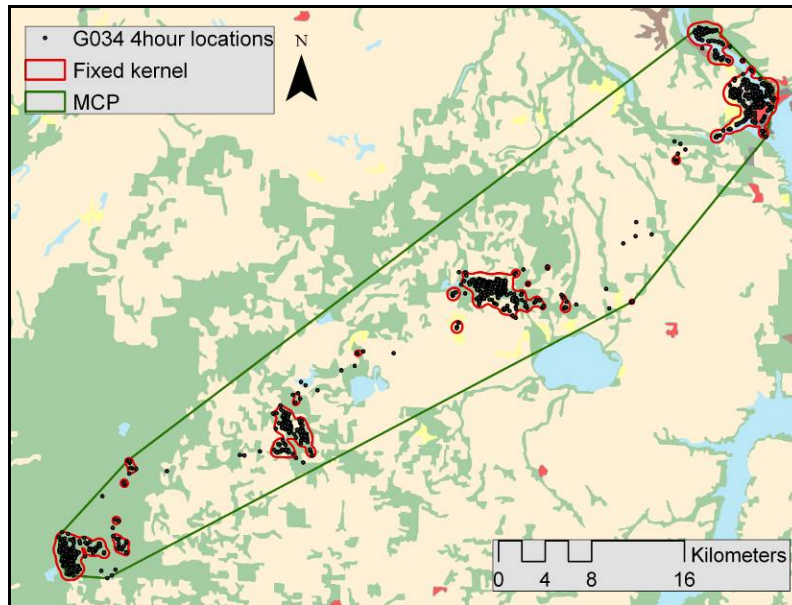


Figure 2.6. Comparison of fixed kernel home range with minimum convex polygon home range for G034, an adult male collared in the Beechy study area. The MCP home range (825 km²) is inflated by long distance movements, while the kernel home range (71.6 km²) includes only the areas regularly travelled by the individual.

Home ranges were calculated for GPS-collared deer surviving longer than 30 days and VHF-collared deer with greater than 20 locations. GPS and VHF home ranges could not be compared because of differences in calculation methods, nor could VHF home ranges be considered in the calculation of average home range size for deer in our study areas. Literature reports that the accuracy of kernel home ranges depends upon number of locations and that at least 30 locations are required to reach asymptote (Seaman et al. 1999). The sample of VHF collared deer for which we collected over 30 locations included only females, so we could not use these in calculations of mean home range size and other descriptive statistics. However, male and female home ranges with greater than 20 locations were used in analyses investigating effects of landscape factors on relative home range size. Time periods over which home ranges

were calculated ranged from 1 month to 3 years, depending on the length of time each individual was present in the study (Table 2.2).

Table 2.2. Total number of GPS-collared (a.) and VHF-collared individuals (b.) included in home range analysis, grouped according to capture year and dataset duration.

a.

Capture year	Dataset duration				Total
	< 0.5 yr	0.5 - 1.0 yr	1.0 - 1.5 yr	1.5 - 2.0 yr	
2007	8	16	2	43	69
2008	4	15	6		25
Total	12	31	8	43	94

b.

Capture year	Dataset duration			Total
	1.5 - 2.0 yr	2.0 - 2.5 yr	2.5 - 3.0 yr	
2006	3	2	29	34
2007	10	14		24
Total	13	16	29	58

Autocorrelation is an issue to be considered in radio telemetry studies (Swihart, Slade 1985, Swihart, Slade 1997). Because locations are taken every four hours for GPS-collared deer, data were considered autocorrelated by the home range software (Swihart, Slade 1985). Deleting random locations until independence is reached (Rodgers, Carr 1998), or using only a subset of locations have been suggested as ways of overcoming this. An unacceptably large percentage of our data had to be removed in order to reach independence, so we chose to accept a degree of autocorrelation in order to avoid decreasing the biological relevance of the resulting home range calculations (de Solla et al. 1999, Blundell et al. 2001).

Least Squares Cross Validation (LSCV) was used to select the appropriate bandwidth for VHF-collared deer data. LSCV is generally accepted as the best method of bandwidth selection (Seaman et al. 1999, Seaman, Powell 1996), but some studies have reported it to be ineffective for their purposes (Blundell et al. 2001). It was found to be problematic when calculating linear home ranges (Blundell et al. 2001), and when dealing with clustered data and high or low sample sizes (Hemson et al. 2005). Due to the clustered nature and large sample sizes of our GPS data, attempts to use LSCV resulted in the software defaulting to the reference bandwidth (h_{ref}) and overestimating home range size. The use of 80% of each h_{ref} value gave reasonable results, but in cases of migratory or dispersal deer, home range sizes were again inflated (Figure 2.7a). As all individuals must be calculated using the same method in order to compare home ranges, this posed a significant problem. Using trial and error, a bandwidth of 275 meters was chosen for use in all calculations. For all types of home ranges in our sample, this bandwidth created contours that closely followed the actual distribution of points while providing a reasonable amount of smoothing, allowing us to accurately compare home range sizes and investigate habitat parameters within each home range (Figure 2.7).

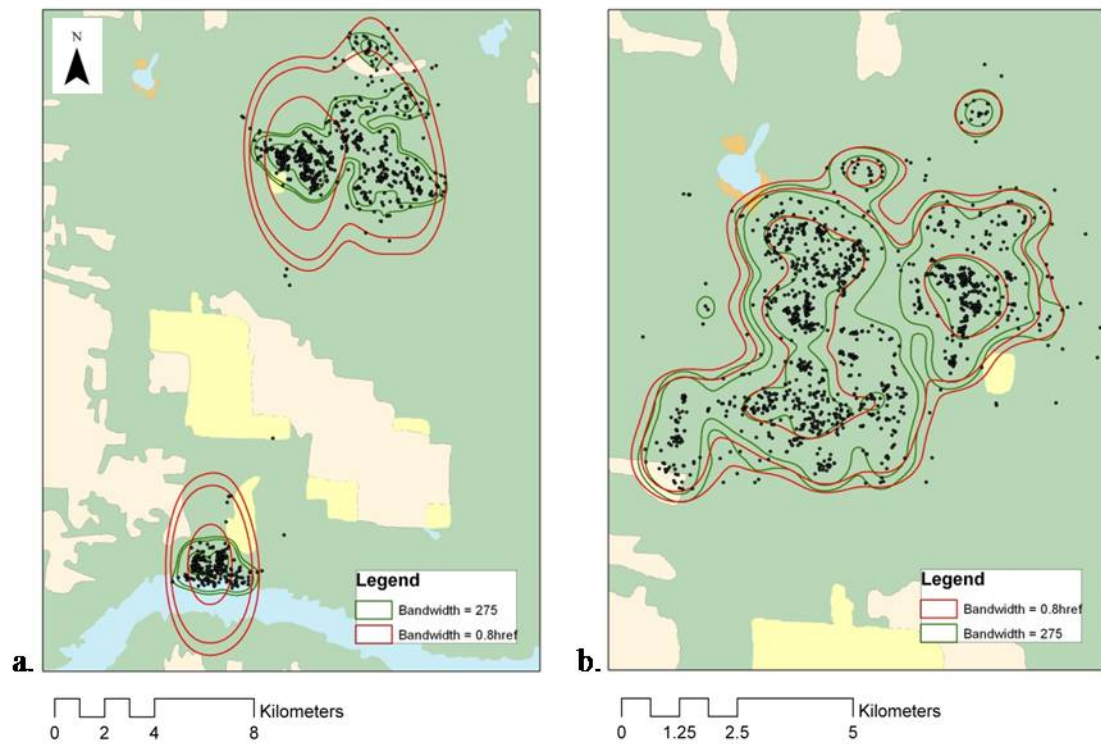


Figure 2.7. Comparison of bandwidths for fixed kernel calculations. A bandwidth of 275m (shown in green) performs well for both migratory (a) and sedentary (b) movement patterns, whereas using 80% of the reference bandwidth (shown in red) results in inflated home ranges for migratory individuals.

CHAPTER 3
LANDSCAPE EFFECTS ON HOME RANGE SIZE OF MULE DEER (*ODOCOILEUS
HEMIONUS*) IN SOUTHERN SASKATCHEWAN: IMPLICATIONS FOR CHRONIC
WASTING DISEASE SPREAD

3.1 Abstract

Home ranges of mule deer have been studied throughout various parts of their range, but little information is available for mule deer in the prairies, and virtually none is available for mule deer in Saskatchewan. Movement patterns such as home range size may be important in influencing rates of disease spread across the landscape. We used GPS and VHF radio collars to calculate fixed kernel home ranges of 154 male and female mule deer from five study sites in and around a chronic wasting disease (CWD) endemic area of southern Saskatchewan. We investigated how home range sizes differ between sexes and how they are influenced by habitat and landscape.

Home ranges (95% fixed kernel) of GPS-collared deer in this study averaged 21.4 km² (n = 94). Male home ranges (\bar{x} = 29.5 km², n = 56) were larger than those of females (\bar{x} = 16.1 km², n = 38), which could have implications for CWD prevalence differences between sexes. The best model for home range size included terrain ruggedness (negatively related) and Shannon's diversity (a measure of both habitat richness and evenness) (positively related), in addition to sex and study site. Also important but not included in the best model were proportion of cropland, average number of habitat patches, and patch size coefficient of variation within home ranges (all positively related). These results suggest that mule deer occupying rugged areas such as creek valleys and coulees may be able to meet their needs within relatively small home ranges,

whereas those with less access to rugged terrain tend to range over larger areas and make use of more diverse, patchy habitats in order to meet their needs.

This research identified relationships between host movement patterns and the surrounding landscape that will help build an understanding of both the temporal and spatial spread of CWD in our study areas. Variation in home range size and movement patterns of mule deer from different areas of North America emphasize the need for region-specific information in order to understand local patterns of disease spread and develop CWD management strategies appropriate to the population in question.

3.2 Introduction

Understanding the movement patterns of a host population is essential in wildlife disease management. Although deer in North America have been studied extensively, little quantitative information exists regarding movements of mule deer in Saskatchewan. Since the identification of chronic wasting disease (CWD) in a free ranging mule deer in Saskatchewan in 2000, management programs have been underway to stop the disease from spreading to other areas of the province. Like many CWD management strategies across North America, these have focused primarily on surveillance and generalized herd reduction by increasing hunting in affected zones. Despite these efforts, CWD has continued to spread beyond the boundaries of the management zones. To date, the disease has been found in white-tailed (*O. virginianus*) and mule deer in 13 wildlife management zones within the province, as well as free-ranging elk (*Cervus elaphus*) in two zones (Saskatchewan Ministry of Environment 2009) and farmed cervids in several areas of the province. Management difficulties are complicated by long-term environmental contamination with prions and uncertainties regarding disease dynamics (Miller et al. 2004, Wasserberg et al. 2009, Miller et al. 2006). Eradication has become a distant goal in some areas

(Williams et al. 2002b), and the most promising areas of management appear to lie in prevention and early detection of spread into new areas (Pybus, Hwang 2008) as well as the development of techniques enabling detection of prions in the environment (Conner et al. 2008).

Mule deer are highly mobile, seasonally gregarious animals, known to exhibit fidelity to a particular home range or set of home ranges (Anderson, Wallmo 1984). Individuals of some populations remain within a single home range for the majority of their lifespan with the exception of a proportion of dispersing juveniles (Eberhardt et al. 1984), while others migrate between a set of seasonal home ranges (Conner, Miller 2004, Brown 1992, Garrott et al. 1987). These patterns of movement will affect the way in which diseases are spread throughout or between host populations and should be incorporated into spatial models predicting the spread of CWD across the landscape (Conner, Miller 2004, Conner et al. 2008). Studies on scales of mule deer movement and CWD dynamics in Colorado determined that heterogeneities in CWD spread across the landscape were best explained at the scale of the individual home range (Farnsworth et al. 2006), suggesting that fine-scale movements and contact patterns are important to consider in attempting to understand or manage disease spread.

The size of an individual's home range may have implications for rates of disease spread across the landscape. Given that CWD can be spread by both direct and indirect contact, a larger home range would expand the area over which an infected individual would shed prions into the environment, or come into contact with susceptible individuals. Many factors have been suggested as influencing home range size in cervids, such as population density (Vincent et al. 1995, Kjellander et al. 2004), forage availability (Relyea et al. 2000, Tufto et al. 1996), sex (Robinette 1966, Relyea et al. 2000), and landscape structure (Kie et al. 2002). Although there is a moderate amount of literature available on home range sizes of mule deer, reports of home

range sizes are difficult to compare due to the wide variety of methods used in calculations of home range as well as the duration of time for which home ranges are reported. Home ranges vary widely among studies, and researchers have reported average mule deer home range sizes ranging from 0.49 km² (*O. h. fuliginatus*, 95% adaptive kernel home range, n = 2)) (Kie et al. 2002) in southern California to 39.8 km² in south central Washington (*O. h. hemionus*, 95% confidence ellipse home range, n = 34) (Eberhardt et al. 1984).

Much of the available literature on mule deer movement is derived from studies undertaken in mountainous areas of the US (Conner, Miller 2004, Relyea et al. 2000, Kie et al. 2002, Kufeld et al. 1988a). Few studies address movements of mule deer in prairie-dominated regions (Wood et al. 1989, Severson, Carter 1978) and no information is available regarding home ranges of mule deer in southern Saskatchewan. To address this, a radio telemetry project was undertaken in 2006 to investigate factors affecting movement patterns of deer in a chronic wasting disease endemic area of southern Saskatchewan. As a component of this project, our objective is to quantify home range patterns of male and female mule deer in this area and identify landscape and habitat factors that may be responsible for determining home range size. The information gained from this study may be used, in conjunction with parallel investigations on migration, dispersal and social structure, to develop predictive models of CWD spread and to inform management decisions in Saskatchewan.

3.3 Methods

3.3.1 Study sites

This research was conducted in five study areas in southern Saskatchewan near the Lake Diefenbaker area of the South Saskatchewan River (Bounded by -108°27'21" and 51°9'46" in the northwest and -106°12'28", 50°24'40" in the southeast) (Figure 3.1). Of the five study areas,

Antelope creek (Antelope), Swift Current Creek (Swift), and the Beechy and Matador community pastures (Beechy and Matador) are within CWD management zones but the most North-easterly site, Douglas Provincial Park (Douglas), is just outside. Douglas is the only site contained within the Moist Mixed Grassland Ecoregion of Saskatchewan, while the other four are within the Mixed Grassland Ecoregion (Acton et al. 1998). The total area covered by all study sites combined is equal to approximately 2700 km², with each site ranging from around 250 to 800 km².

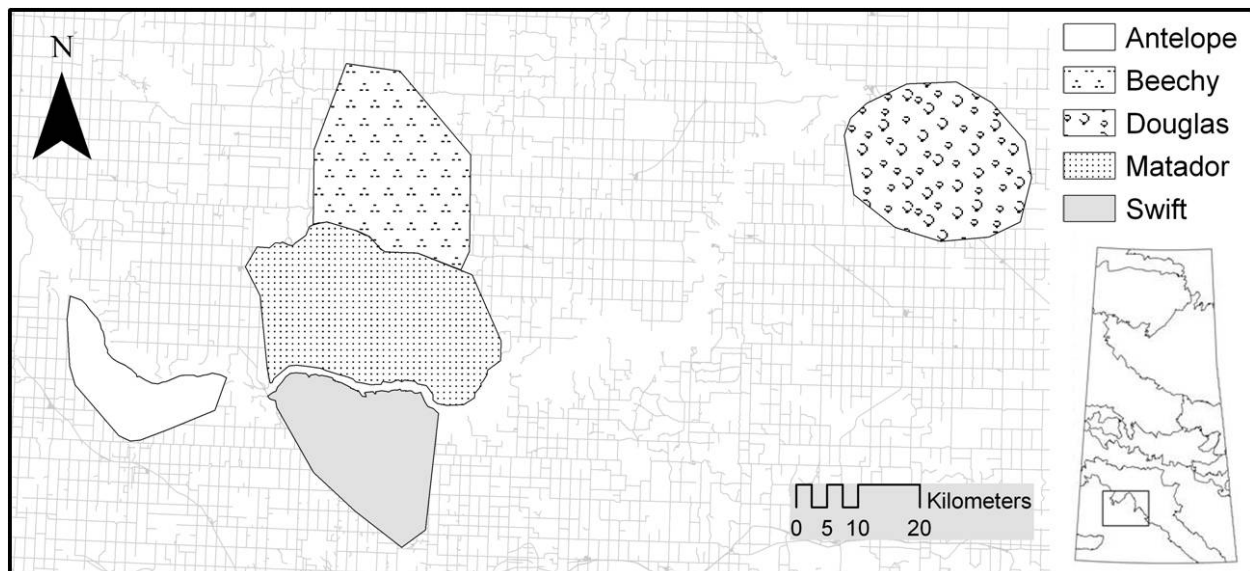


Figure 3.1. Locations of study sites in southern Saskatchewan.

The Mixed Grassland Ecoregion is characterized by a semiarid climate with mean annual precipitation of 352 mm, mean July temperature of 18.9°C and mean January temperature of -12.6°C (Acton et al. 1998). Annual cropland makes up a major proportion of the study sites, while the remaining habitat is composed mostly of mixed grass prairie across rolling pastureland and through the river valley and deciduous shrubs in coulees and low lying areas (Figure 3.2).

Very little forest cover is present except in the Douglas study site, where patches of aspen (*Populus tremuloides*) forest and deciduous shrubs are dispersed among pasture and sand hills habitats. Common annual crops of this region are barley, durum, wheat, oats, canola, peas and lentils (Saskatchewan Ministry of Agriculture 2008). Please refer to general materials and methods for a more detailed description of the study sites.

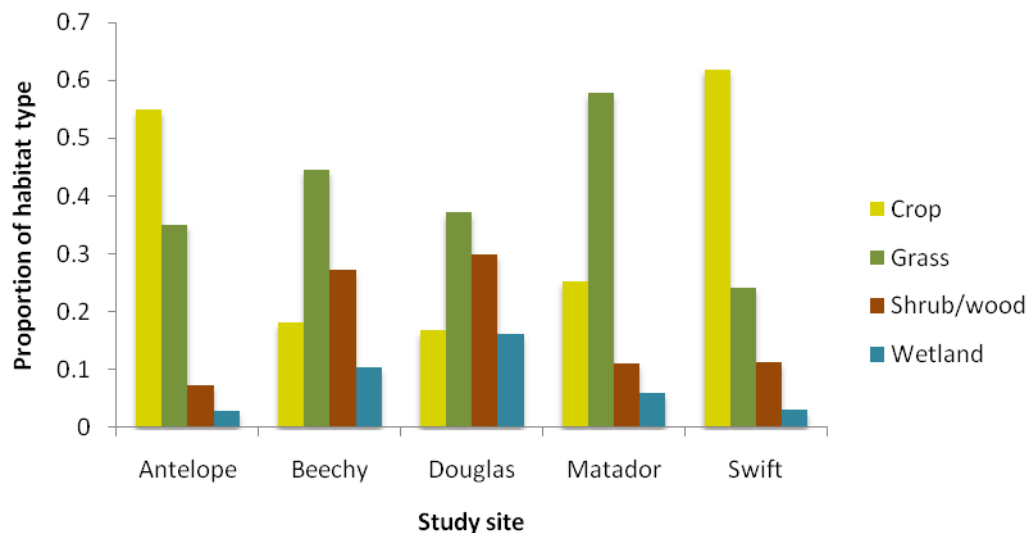


Figure 3.2. Proportional contribution of each land cover type to the total area of each study site.

3.3.2 Capture and radio telemetry

Deer were captured between January and April of 2006, 2007 and 2008 using either clover traps (Clover 1956) or a helicopter and net gun (Barrett et al. 1982). Clover traps were modified following McCullough (1975) and trap height was increased to 50" to allow for capture of adult bucks. All deer were chemically immobilized with intramuscular injections of combined Telazol® and Xylazine (Rompun®) and reversed with Atipamezole (Antisedan®) after collar deployment and sample collection. Animal handling protocol was approved by the Animal Care

and Use Committee. Each deer was fitted with a VHF collar (LOTEK, ATS) or a GPS collar (LOTEK, Televilt) programmed to take automatic fixes every 1-8 hours. Male collars were fitted with specially designed foam inserts to allow for neck swelling during the rut.

VHF-collared deer were tracked on a monthly basis between 2006 and 2009 by small aircraft or on the ground on foot or by truck, ATV or snowmobile. GPS-collared deer were also tracked regularly between 2007 and 2009 to identify long distance movements and to periodically download data from UHF-equipped collars. Collars were retrieved during February and March of 2009. To avoid bias due to higher sampling frequency during particular seasons, only GPS fixes taken at 4, 8, 12, 16, 20, and 24 hours local mean time (LMT) were used for analysis, excluding zero values and erroneous or suspect data points. Data collected within the first two weeks following capture were also removed to avoid the inclusion of capture-related movement changes in the analysis.

3.3.3 Home range size

Fixed kernel home ranges were calculated for GPS-collared deer surviving longer than 30 days and VHF-collared deer with greater than 20 locations using Home Range Tools (HRT) (Rodgers et al. 2007) for ArcGIS (ESRI 2007). This extension uses a bivariate normal kernel estimation to build a raster of probability values based on the utilization distribution (UD) of all locations for an individual, with each cell value representing the likelihood that an individual may be located in that particular cell over a period of time (Kernohan et al. 2001). Unlike minimum convex polygons (MCP), kernel estimation allows for exclusion of brief excursions and distinction between seasonal home ranges of migratory individuals. Grid resolution was set at 50 m and contours delineating 95% of estimated UD were used in the calculation of home

range size. Time periods over which home ranges were calculated ranged from 1 month to 3 years, depending on the length of time each individual was present in the study.

Least Squares Cross Validation (LSCV) was used to select appropriate bandwidth for VHF-collared deer data. However, due to the clustered nature and large sample sizes of GPS data, attempts to use LSCV resulted in calculations defaulting to the software-generated reference bandwidth (h_{ref}) and overestimating home range size. Using trial and error, a bandwidth of 275 m was chosen for use in all calculations involving GPS data. This bandwidth created contours that closely followed the actual distribution of points while providing a reasonable amount of smoothing, allowing us to accurately compare home range sizes and investigate habitat parameters within each home range.

Autocorrelation was also an issue to be considered in the calculation of home ranges (Swihart, Slade 1985, Swihart, Slade 1997). Because locations were taken every four hours for GPS-collared deer, data were considered autocorrelated according to the home range software (Swihart, Slade 1985). Excluding random locations until independence is reached (Rodgers, Carr 1998), or using only a subset of locations have been suggested as ways of overcoming this. An unacceptably large percentage of our data had to be removed in order to reach independence; therefore we chose to accept a degree of autocorrelation in order to avoid decreasing the biological relevance of the resulting home range calculations (de Solla et al. 1999, Blundell et al. 2001).

3.3.4 Landscape classification

A classified land cover map was created for the five study areas using 20 m resolution, multispectral SPOT (Satellite Pour l'Observation de la Terre) images obtained during July and September of 2007 (Alberta Terrestrial Imaging Centre 2007). Raw images were orthorectified

using PCI Geomatica software (PCI Geomatics 2005) and were not radiometrically processed. Images covering the Swift, Matador, Beechy and Antelope study sites were collected within the same time period (July 2007), which allowed us to mosaic the images and classify them together. Collection of one image relevant to the Douglas study area was delayed until September 2007, so this image was classified separately due to spectral differences.

Vegetation training data were collected along transects in each study area throughout the summer of 2007 in conjunction with a deer population survey. Each location of field data collection was overlaid with SPOT imagery and the associated pixel or pixels were classified as the land cover type documented at that location. Additional training sites were identified and classified through visual interpretation of the 20 m SPOT imagery and high resolution (2.5 m) panchromatic SPOT imagery (Telus 2006), guided by knowledge of the area obtained during field activities. Only locations that could be classified with a high level of certainty were used as supplementary training sites. Thirty percent of all training or “ground truth” polygons were withheld as reference data for accuracy assessment, while the remaining 70% were used as training locations for the classification process.

Digital elevation model (Government of Canada, Natural Resources Canada, Earth Sciences Sector, Centre for Topographic Information 2000-2009) and terrain ruggedness layers (Evans 2004) (both 25 m resolution) were used to supplement remotely sensed imagery and add a topographic dimension to the classification. These layers were stacked with the SPOT images, along with an additional layer created by applying a homogeneity filter to the SPOT near infrared band. Pixel size was resampled to 25 m and supervised classification was performed within ENVI software (ITT Visual Information Solutions 2008) using a maximum likelihood classifier. Resolution of the final product was 25 m.

The original classification scheme consisted of nine classes: crop, grassland, mixed grass/shrub, shrub, woodland, wetland, open water, unvegetated, and unclassified; However, due to difficulties distinguishing between certain classes, the image was reclassified using only five classes. As the mixed grass/shrub class was created to represent low lying shrub habitats dominated by grasses, this class was combined with the grassland class. The shrub and woodland classes were combined because of the relative lack of woodland throughout all areas except Douglas, and the resulting lack of woodland training locations. Annual cropland and perennial forage crop were classified together and combined with the unvegetated class because the vast majority of unvegetated areas were associated with unplanted or cut cropland. Open water and wetland classes were combined into one class as well. The final, broad classification scheme was accepted for the purposes of this study due to its biological relevance to mule deer behaviour.

3.3.5 Landscape characterization within home ranges

Proportions of each habitat type and average terrain ruggedness index (TRI) and elevation values were calculated for each home range using Hawth's tools (Beyer 2007) extension for ArcGIS. Landscape metrics were then calculated using Patch Analyst Extension (Rempel et al. 2000), which was developed for the ArcGIS platform based on FRAGSTATS software (McGarigal, Marks 1994). These metrics include diversity, evenness, mean shape index, perimeter area ratio, mean patch fractal dimension, mean and median patch size, patch density, edge density, mean patch edge, and standard deviation and coefficient of variance for patch size (Table 3.1)

Table 3.1. Landscape metrics investigated using Patch Analyst. Adapted from (Elkie 1999) and (McGarigal 1994).

Landscape metric	Description
Number of patches	Total number of patches
Mean patch size	Average size of all habitat patches
Median patch size	Middle value of all patch sizes
Patch size standard deviation	Standard deviation of all patch sizes
Patch size coefficient of variance	Coefficient of variance of all patches
Total edge	Sum of perimeters of all patches
Edge density	Total edge divided by home range size
Mean patch edge	Average amount of edge per patch
Mean perimeter-area ratio	A measure of shape complexity: Sum of the perimeter/area ratio of each patch divided by the total number of patches
Mean shape index	A measure of shape complexity: sum of each patch's perimeter divided by the square root of patch area, adjusted for circular standard and divided by the number of patches
Mean patch fractal dimension	A measure of shape complexity: Value approaches one for shapes with simple perimeters and two for more complex shapes
Area weighted mean shape index	Mean shape index weighted by the size of each patch
Area weighted mean patch fractal dimension	Mean patch fractal dimension weighted by the size of each patch
Diversity	Shannon's diversity index: Relative measure of patch diversity – the index equals zero when there is only one patch in the landscape and increases as the number of patch types or proportional distribution of patch types increases
Evenness	Shannon's evenness index: Measure of patch distribution – equal to zero when the patch distribution is low and approaches one when the distribution of patch types becomes more even.

Certain landscape metrics, such as mean patch size, amount of edge, and number of patches should not be analyzed at the home range scale because they are dependent on home range size (Kie et al. 2002). To avoid this problem, studies have calculated landscape metrics by creating circular polygons at set radii around each home range centroid and investigating the relationship between resulting values and home range size (Kie et al. 2002, Anderson et al.

2005). Although this method may be preferable for many home range studies, the long distance migration paths of deer in several of our study areas prevented us from choosing a radius that would encompass both home ranges of migratory deer while providing a biologically appropriate scale for analysis. As an alternative, we generated a network of hexagonal polygons, each with an area of 200 ha across the entire habitat map and calculated landscape metrics within each hexagonal polygon. These polygons were then joined with the overlapping home ranges, and values for each landscape metric were calculated for each home range by averaging values associated with overlapping hexagons. Diversity and evenness could be considered size dependent if the minimum home range size and the minimum habitat patch size were similar, but in this analysis, where the minimum patch size was 30 m and the smallest home range was greater than 2 km, there was opportunity for even the smallest home range to encompass a range of habitat types. Therefore, diversity and evenness were determined to be size independent and were calculated within each home range polygon.

3.3.6 Statistical analysis

Differences in home range size between males and females and between study sites were investigated using SPSS (SPSS Inc. 2008). Two-way ANOVA (Analysis of Variance) was used to look at differences between sexes and study sites and post-hoc comparisons were performed using t-tests. Data were normally distributed and met all assumptions with the exception of equal variances between males and females.

Mixed model regression was performed using SAS PROC MIXED (SAS Institute 2002) to determine which parameters were important in determining home range size. Sex, collar type, and site were tested as fixed effects with each landscape and habitat parameter, and interactions were tested for all significant parameters. A correlation matrix was generated in SPSS to identify

non-independent factors that could not be placed in the same model. Significant habitat and landscape metrics, along with sex, study area, and collar type were placed in a model and least significant variables were removed until all remaining variables were significant. Models were compared and the best was chosen based on AIC (Akaike Information Criteria) values.

Because temporal period of home ranges differed among individuals, we performed mixed model regression to determine whether this factor affected GPS-collar or VHF-collar home ranges. Fix success of and proportion of 3D locations were also calculated for each GPS collar using raw data. These factors were tested to determine whether they created bias in calculating home range size.

To address the question of whether home range sizes were limited by the amount of continuous natural habitat available, we also compared two subsets of home ranges from Swift Current Creek and the southern region of Matador, two areas with comparable topography but differing amounts of continuous habitat (Figure 3.3). For this analysis, we selected home ranges with TRI values greater than 5.0 from each site. To eliminate bias related to sex and collar type, we randomly removed individuals from over-represented classes until sex and collar proportions were similar between the two groups. We then tested for normal distribution of groups and performed a t-test to determine whether home range sizes differed between the two areas with similar topographic characteristics.

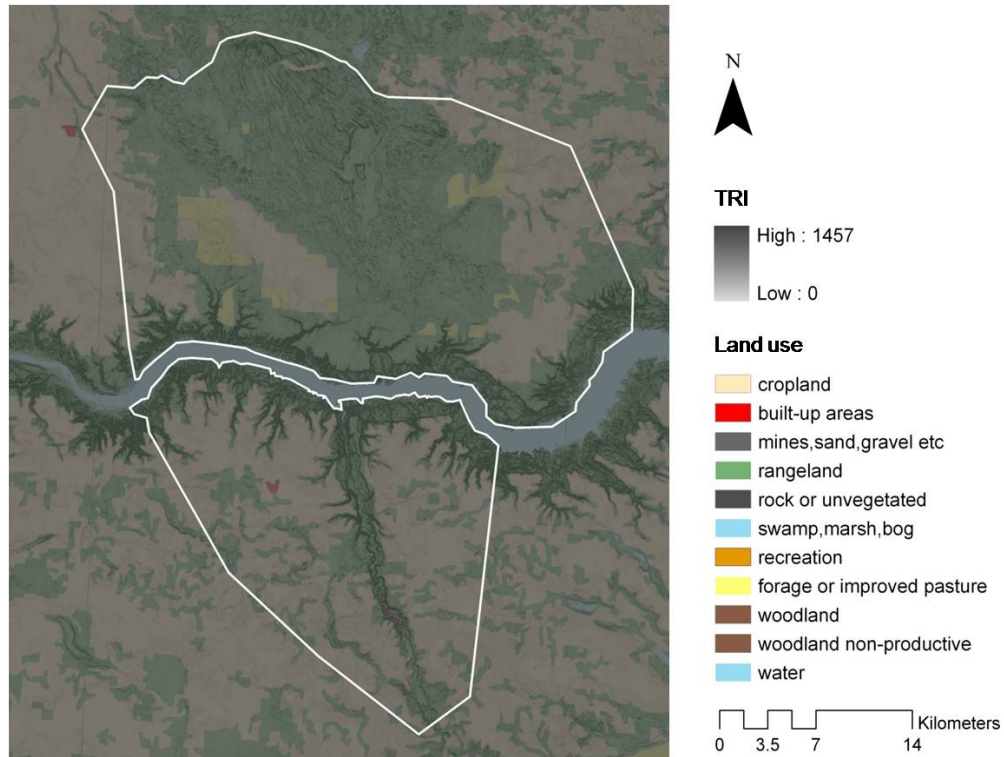


Figure 3.3. Comparison between the Matador (top) and Swift (bottom) study areas. The south end of Matador has a similar degree of terrain ruggedness (TRI) to that of Swift, but a greater amount of continuous natural habitat.

3.4 Results

3.4.1 Dataset

A total of 152 deer were included in the analysis, 94 of which were GPS-collared (56 male; 38 female) and 58 of which were VHF-collared (17 male; 41 female). Time periods over which home ranges were calculated ranged from 1 month to 3 years, depending on the length of time each individual was present in the study (Table 3.2). Mean number of locations available was 32 (range = 20 - 43) for VHF-collared deer and 2384 (range = 167 - 4361) for GPS-collared deer.

Table 3.2. Number of GPS-collared (a) and VHF-collared (b) individuals included in the study summarized by capture year and duration of time over which home ranges were calculated.

a.

Capture year	Dataset duration				Total
	< 0.5 yr	0.5 - 1.0 yr	1.0 - 1.5 yr	1.5 - 2.0 yr	
2007	8	16	2	43	69
2008	4	15	6		25
Total	12	31	8	43	94

b.

Capture year	Dataset duration			Total
	1.5 - 2.0 yr	2.0 - 2.5 yr	2.5 - 3.0 yr	
2006	3	2	29	34
2007	10	14		24
Total	13	16	29	58

3.4.2 Home range size

3.4.2.1 Effects of dataset duration and collar success

Temporal duration over which home ranges were calculated did not affect home range size for VHF-collared deer used in the study ($F_{1,51} = 0.97$, $p = 0.331$). However, duration was positively related to home range size for GPS-collared deer ($F_{1,87} = 12.71$, $p < 0.001$). To ensure this did not create bias in results, interactions were tested between duration and all significant influencing factors. The interaction with sex was significant ($F_{1,86} = 4.41$, $p = 0.039$), but sex did not affect duration of dataset ($F_{1,88} = 0.12$, $p = 0.727$) when duration was tested as a dependent factor. No other interactions were significant, nor were the effects of proportion of successful fix attempts ($F_{1,87} = 0.14$, $p = 0.712$) and proportion of 3D fixes ($F_{1,87} = 3.27$, $p = 0.074$) on home range size.

3.4.2.2 Effects of sex and study site

The overall mean of home range size was 24.1 km² (SE = 1.7, range = 2.1 - 87.7 km², n = 94) (Table 3.3), with females having smaller home ranges than males ($t_{89.8} = -4.56$, $p < 0.001$). Average male home range size was 29.5 km² (SE = 2.5, range = 2.1 - 87.7 km², n = 38) which was nearly twice the female average of 16.1 km² (SE = 1.6, range = 4.8 – 51.5 km², n = 56). There were significant differences between study areas as well ($F_{4,89} = 4.68$, $p = 0.002$), but no interaction between sex and study site (Figure 3.5). The largest differences between study areas were between Swift and Matador ($t_{28.1} = -3.51$, $p = 0.002$) and Beechy and Swift ($t_{30} = 3.58$, $p = 0.001$), with home ranges in Swift ($\bar{x} = 16.0$ km², SE = 2.0 km², n = 25) smaller than those in Matador ($\bar{x} = 33.9$ km², SE = 4.7 km², n = 21) and Beechy ($\bar{x} = 33.8$ km², SE = 6.5 km², n = 7) (Table 3.3). Swift home ranges were also smaller than those in Antelope ($t_{50} = -2.34$, $p = 0.023$), but there were no other significant differences between study areas. Differences between age classes were not investigated because of inadequate juvenile sample sizes and complications in dealing with changes in age classes over time.

Table 3.3. Mean ($\bar{x} \pm 1\text{SE}$) 95% kernel home range size (km²) and number (n) of individuals overall and for GPS-collared males and females in each of the five study areas. Significant differences exist between Swift and Antelope, Beechy, and Matador.

Study site	Home range size					
	Male			Female		
	$\bar{x} \pm 1 \text{ SE}(\text{km}^2)$	n		$\bar{x} \pm 1 \text{ SE}(\text{km}^2)$	n	Overall
Antelope	27.5 \pm 3.3	18		15.6 \pm 2.1	9	23.5 \pm 2.5
Beechy	47.5 \pm 24.0	2		28.3 \pm 2.2	5	33.8 \pm 6.5
Douglas	27.6 \pm 6.7	8		9.35 \pm 1.4	6	19.8 \pm 4.5
Matador	36.3 \pm 5.6	16		25.7 \pm 7.4	5	33.9 \pm 4.7
Swift	21.3 \pm 3.1	12		11.0 \pm 1.5	13	16.0 \pm 2.0
Overall	29.5 \pm 2.5	56		16.1 \pm 1.6	38	24.1 \pm 1.7

Table 3.4. Distribution of kernel home range data (km²) for GPS-collared deer in each study area.

Study site	n	Min	Percentiles			Max
			25th	50th	75th	
Antelope	27	6.44	14.2	19.3	29.1	57.2
Beechy	7	22.2	23.5	27.6	35.1	71.6
Douglas	14	2.12	7.82	10.4	34.2	52.0
Matador	22	4.18	15.6	29.9	46.4	87.7
Swift	25	4.75	8.30	13.0	20.9	43.6

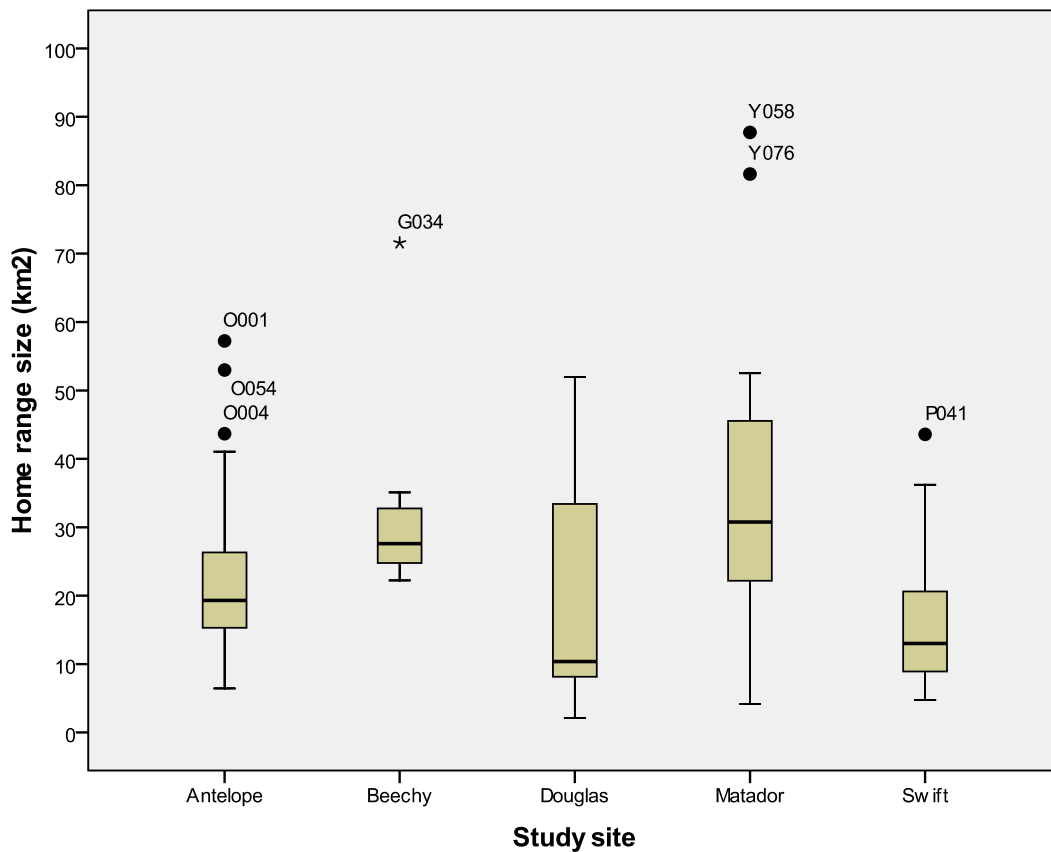


Figure 3.4. Distribution of kernel home range data (km²) for GPS-collared deer in each study site. Shaded boxes indicate data between the 25th and 75th percentiles, with the median indicated by a horizontal line. Whiskers represent all remaining data within 1.5 box-lengths of the 25th and 75th percentiles. Outliers (dots) are values falling outside of this distribution and extreme values (stars) are greater than 3 box lengths from the 25th or 75th percentile.

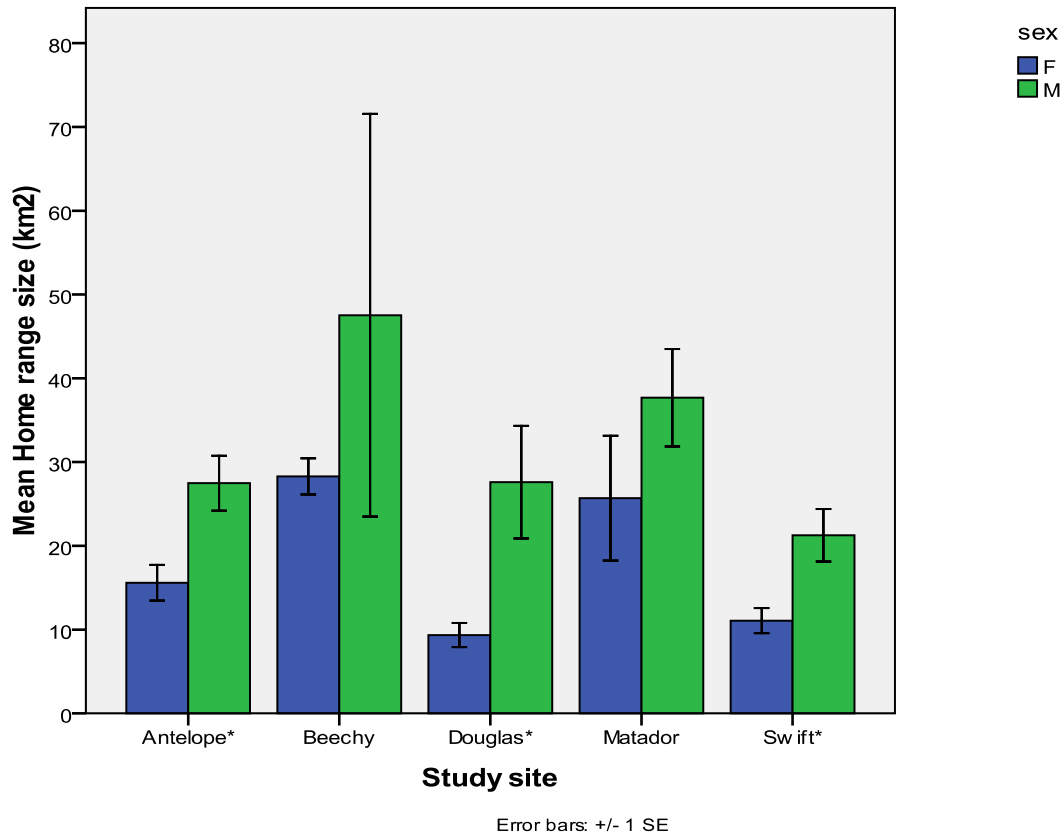


Figure 3.5. Mean 95% kernel home range sizes (km²) of GPS-collared deer by sex and study area. Stars indicate significant differences between males and females ($\alpha = 0.05$).

3.4.2.3 Effects of habitat and landscape

Habitat composition within home ranges significantly influenced mule deer home range size. Larger home ranges tended to contain greater proportions of cropland ($F_{1,144} = 5.48$, $p = 0.021$), but grassland ($F_{1,144} = 3.17$, $p = 0.077$), wetland ($F_{1,144} = 2.01$, $p = 0.159$) and shrub/woodland ($F_{1,144} = 2.80$, $p = 0.097$) did not significantly affect home range size.

Topography was an influencing factor as home range size was negatively related to terrain ruggedness ($F_{1,144} = 23.04$, $p < 0.001$) (Figure 3.6a).

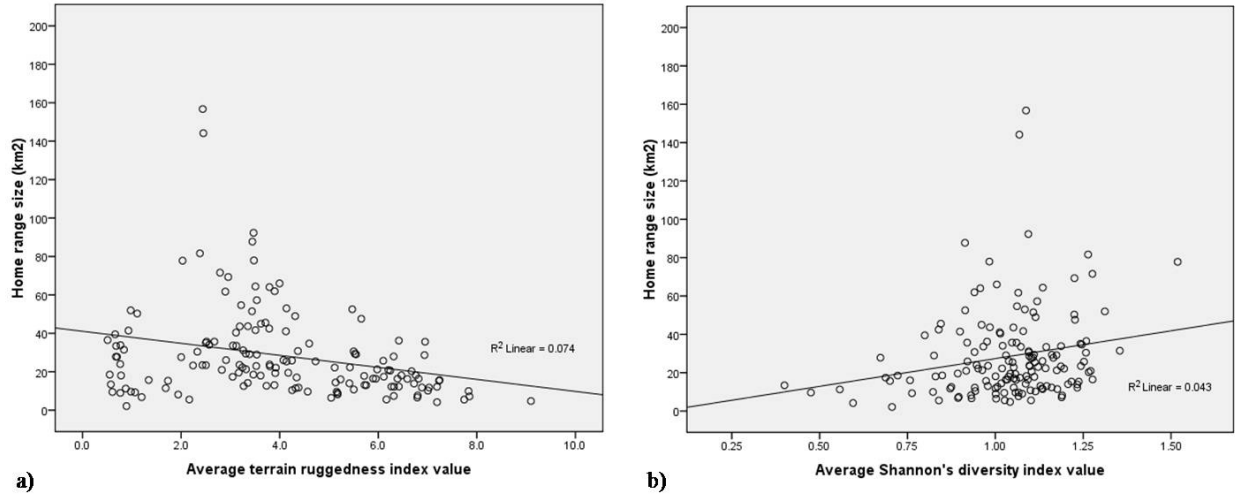


Figure 3.6. Relationships between home range size (km²) and terrain ruggedness index (TRI) (a) and Shannon's diversity index (SDI) (b).

Several measures of landscape heterogeneity were tested individually to determine which were important to consider in a model of home range influences. Of a total of 14 possible landscape metrics, four were found to be significantly related to home range size. Diversity ($F_{1,144} = 9.48$, $p = 0.003$) (Figure 3.6b), evenness ($F_{1,144} = 6.63$, $p = 0.011$), average number of patches ($F_{1,144} = 5.96$, $p = 0.016$), and patch size coefficient of variation ($F_{1,144} = 6.06$, $p = 0.015$) were all positively related to home range size. Diversity and evenness were highly correlated ($r = 0.943$, $p < 0.001$). This was expected because they are similar measures, diversity being a measure of both the number and proportional contribution of habitat types present, and evenness being a measure of only the proportional contribution of habitat types present. Each was tested separately in a different model.

Sex and proportion of crop had interacting effects on home range size ($F_{1,143} = 4.47$, $p = 0.036$). When males and females were investigated separately, proportion of crop was positively related to male home range size ($F_{1,67} = 5.61$, $p = 0.021$), but not significantly related to female

home range size ($F_{1,73} = 1.34$, $p = 0.250$). There were no other interactions between sex, site, or collar type and any of the significant landscape or habitat factors. The model that best explained variation in home range size included topographic ruggedness and diversity, in addition to sex, site, and collar type (Table 3.5). According to this model, home ranges tended to be larger in areas of gentle terrain with a greater number and proportional contribution of habitat types.

Table 3.5. Akaike Information Criteria (AICc) values, change in AICc (Δ_{AICc}), and residual error of models used to explain variation in home range size.

Variables in model	AIC_c	Δ_{AICc}	Residual error
Ruggedness, diversity, sex, site, collar type	1255.1	0.0	303.5
Ruggedness, evenness, sex, site, collar type	1256.1	1.0	307.3
Null model	1386.4	131.3	542.9

Additional home range subsets were compared between the Swift study area and the southernmost region of the Matador study area. These two groups of home ranges contained similar amounts of rugged terrain (Average TRI values were 6.23 and 6.28 for Matador and Swift, respectively) but were surrounded by differing amounts of continuous habitat. Average home range sizes for the Matador and Swift subsets were 16.6 km² ($n = 10$, $SE = 4.37$) and 18.5 km² ($n = 20$, $SE = 1.63$), respectively. Home ranges were not significantly different ($t_{11.6} = 0.413$, $p = 0.687$) between the two sites, which suggested that terrain ruggedness may be more important than continuous natural habitat in determining home range size.

3.5 Discussion

As in other studies investigating the effects of landscape on movement patterns and distribution of deer, we found that landscape composition significantly influenced home range sizes of mule deer in our study areas. Landscape heterogeneity (of which Shannon's Diversity

Index is one measure) was expected to be negatively related to home range size, as a greater variety of habitat types in an area may allow an individual to meet its needs within a smaller range (Kie et al. 2002). Our results were not consistent with this expectation, as higher diversity values tended to be associated with larger home ranges. However, this relationship agreed with that of mule deer occupying a similar prairie habitat in Montana, where authors explained that deer compensated for a lack of available hardwood draws and badlands habitat by expanding their home range to include a variety of habitats (Wood et al. 1989).

The association between smaller home ranges and topographic ruggedness supports this explanation and highlights the importance of rugged terrain in grassland-dominated environments where forest cover is scarce (Lingle 2002, Wood et al. 1989, Lingle 2003, Swenson 1982, Dusek 1975). Rugged terrain in southern Saskatchewan occurs mostly in the form of draws, coulees, and river or creek valleys with shrubby vegetation along the bottom, often surrounded by unvegetated cliffs. These features provide mule deer with concentrated sources of forage, as well as protection from predation and winter elements. Mule deer with less access to this type of habitat may need to range over larger areas in order to access other sources of forage and protective cover.

Study site differences prompted further questions regarding the importance of available continuous habitat in determining home range size. Beechy and Matador, the areas containing the largest home ranges on average, are composed of one large, continuous expanse of grassland that meets the river to the south, whereas Swift, the area in which the smallest home ranges were found, is made up of a creek valley and networks of rugged coulees surrounded by cropland. The effect of surrounding cropland is difficult to measure directly as it would require analysis at larger scales to identify habitat influences acting outside of the home range. We chose to address

this question indirectly, by determining if a sample of home ranges selected from the rugged south end of Matador would differ significantly in size from those in Swift Current Creek. Results from this analysis showed that the two subsets of home ranges with similar ruggedness values did not differ significantly in size, suggesting that available continuous habitat may not be as important as topographic ruggedness in determining home range size in mule deer.

It is difficult to compare results of studies on mule deer home range size because of the wide variety of methods used to estimate an animal's home range. Even using the same dataset, different methods may output very different results, which emphasizes the importance of clearly stating methods used when reporting home range size (Harris et al. 1990). Despite these difficulties, home range sizes of mule deer in our study areas are larger than those reported in the majority of the literature (Wood et al. 1989, Nicholson et al. 1997, Robinette 1966, Relyea et al. 2000, Kie et al. 2002). We did not include VHF-collared deer in our reports of average home range size because of the potential for inaccuracies and insufficient numbers of data points, but it is important to note that home ranges of VHF collared deer ranged as high as 156.7 km² (Table 3.6). In addition, the calculation of 100% minimum convex polygons (MCP) for all deer used in this study averaged 115.5 km² (SE = 19.9 km²) (Table 3.7) and ranged as high as 2519.6 km² (Table 3.8) (The MCP home range of an adult doe from the Swift study area whose unusual long-distance movements were not reflected in the kernel estimation of her home range) (Figure 3.8). Although MCP estimation was not appropriate for landscape analysis due to the inclusion of unused or rarely-used areas, particularly for migratory individuals, it does provide perspective on the total area, rather than only regularly used areas, that may be covered by the movements of an individual mule deer. This additional information may be important to consider for wildlife

disease management when home range sizes are included in models of disease spread and used to determine suitable scales at which to implement management strategies.

Table 3.6. Mean ($\bar{x} \pm 1\text{SE}$) kernel home range size (km^2) and number (n) of individuals of VHF-collared deer with greater than 20 locations in each of the five study areas.

Study site	Home range size					
	Male			Female		
	$\bar{x} \pm 1 \text{ SE}(\text{km}^2)$	n		$\bar{x} \pm 1 \text{ SE}(\text{km}^2)$	n	Overall $\bar{x} \pm 1 \text{ SE}(\text{km}^2)$ n
Antelope	47.9 \pm 21.8	6		16.5 \pm 3.7	4	35.4 \pm 13.7 10
Beechy	79.8 \pm 33.2	3		58.7 \pm 7.8	9	64.0 \pm 9.5 12
Douglas	25.9 \pm 3.3	4		22.6 \pm 4.6	8	23.7 \pm 3.2 12
Matador	N/A \pm N/A	0		37.9 \pm 8.4	8	37.9 \pm 8.4 8
Swift	35.9 \pm 4.5	4		16.2 \pm 3.7	12	21.1 \pm 2.7 16
Overall	45.6 \pm 9.9	17		31.0 \pm 3.6	41	35.3 \pm 3.9 58

Table 3.7. Mean ($\bar{x} \pm 1\text{SE}$) minimum convex polygon (MCP) home range size (km^2) and number (n) of individuals overall and for males and females in each of the five study areas.

Study site	Home range size					
	Male			Female		
	$\bar{x} \pm 1 \text{ SE}(\text{km}^2)$	n		$\bar{x} \pm 1 \text{ SE}(\text{km}^2)$	n	Overall $\bar{x} \pm 1 \text{ SE}(\text{km}^2)$ n
Antelope	117.0 \pm 36.9	24		58.3 \pm 18.9	13	96.4 \pm 25.1 37
Beechy	210.3 \pm 153.9	5		141.1 \pm 29.7	14	159.2 \pm 43.7 19
Douglas	90.5 \pm 22.6	12		23.9 \pm 3.9	14	54.6 \pm 12.34 26
Matador	153.7 \pm 28.0	17		174.1 \pm 40.2	13	162.5 \pm 23.2 30
Swift	103.9 \pm 63.1	16		124.7 \pm 100.2	25	116.6 \pm 65.2 41
Overall	124.6 \pm 21.7	74		107.0 \pm 33.0	79	115.5 \pm 19.9 153

Table 3.8. Distribution of MCP home range data (km^2) for GPS and VHF-collared mule deer in each study area.

Site	n	Min	Percentiles			Max
			25th	50th	75th	
Antelope	37	9.42	24.8	62.6	109.8	938.8
Beechy	19	19.8	46.0	98.7	197.4	825.2
Douglas	26	5.26	14.3	22.0	97.6	191.0
Matador	30	3.78	55.9	160.4	228.8	560.5
Swift	41	4.49	10.6	20.3	35.1	2519.6

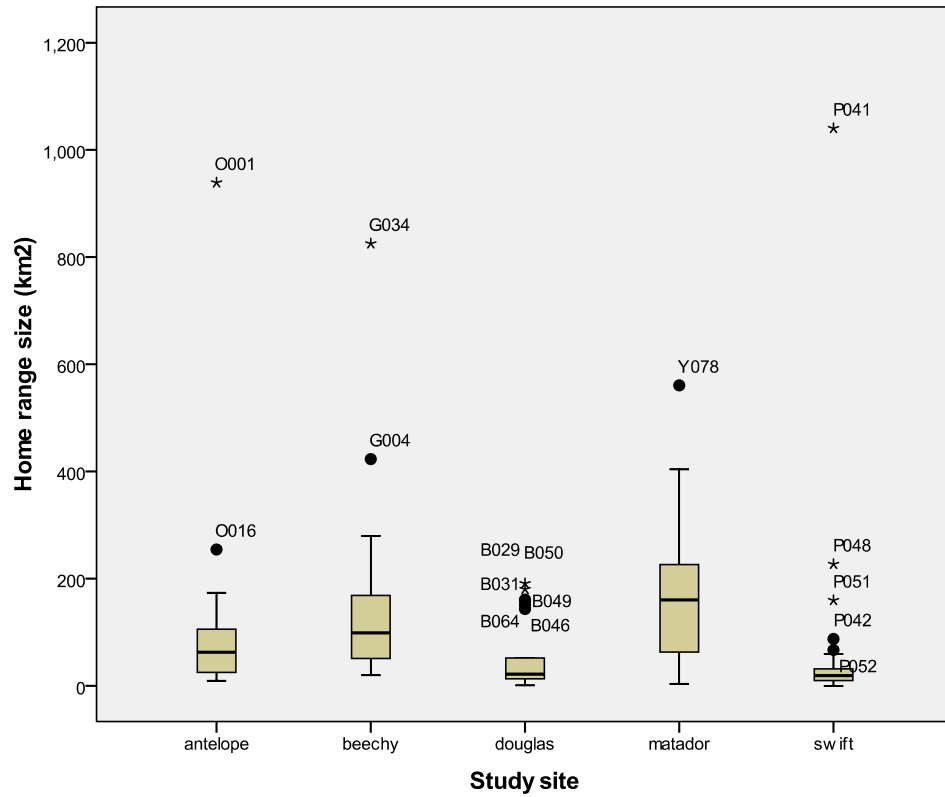


Figure 3.7. Distribution of MCP home range data (km²) for GPS and VHF-collared deer in each study area (P012 not shown). Boxes indicate data between the 25th and 75th percentiles, with the median indicated by a horizontal line. Whiskers represent all remaining data within 1.5 box-lengths of the 25th and 75th percentiles. Outliers (dots) are values falling outside of this distribution and extreme values (stars) are greater than 3 box lengths from the 25th or 75th percentile.

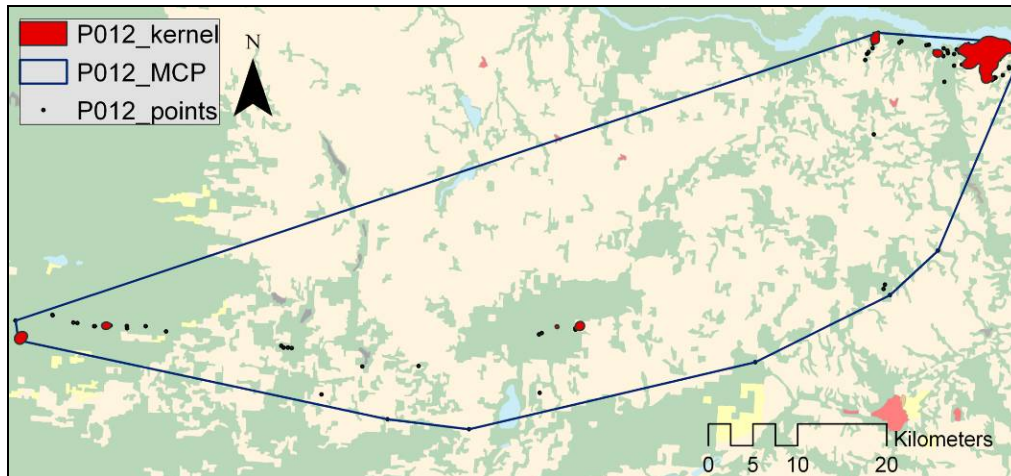


Figure 3.8. The MCP home range (area = 2519.6 km²) of an adult female mule deer collared in the Swift study area whose unusual long distance movements were not reflected in the estimation of her kernel home range (area = 22.3 km²).

Sex-based differences in home range sizes of mule deer are also important to quantify, particularly in the context of understanding wildlife disease. The finding of larger male home ranges in this study agrees with the results of other studies (Robinette 1966, Relyea et al. 2000) and may have implications for chronic wasting disease. Higher CWD prevalence in male deer has been found in regions affected by the disease, including southern Saskatchewan. Reasons for this are uncertain, but are thought to involve differences in exposure to the disease agent rather than differences in susceptibility among sexes (Miller, Conner 2005). This may be due in part to breeding and non-breeding related social behaviour (Farnsworth et al. 2006, Miller, Conner 2005), but larger home ranges may also play a role by increasing the potential for direct and indirect exposure of adult male mule deer to infectious prions.

3.6 Conclusion and management implications

Spatial models predicting patterns of disease spread throughout wildlife populations require baseline information on home range and other movement patterns relevant to the

population in question. Home range information has been collected for deer in many regions throughout North America, but none was previously accessible regarding mule deer in this chronic wasting disease-endemic area of southern Saskatchewan. Not only will region-specific information allow us to create a relevant pool of knowledge on which to base disease models, but it will also enable us to identify commonalities with deer populations in other geographic areas. This will help to guide information sharing with researchers and managers in areas with longer histories of CWD management, as well as those at risk but not yet affected by the disease.

It has also been shown that habitat use plays a role in fine-scale heterogeneities of CWD spread (Farnsworth et al. 2006). The incorporation of landscape and habitat factors into models of disease spread has been useful in enhancing the understanding of other wildlife-associated diseases such as bovine tuberculosis (*Mycobacterium bovis*) (McKenzie et al. 2002, Brook, McLachlan 2009), parapoxvirus (Rushton et al. 2000), and fox rabies (Deal et al. 2000). Our research has identified relationships between host movement patterns and the surrounding landscape that will help us to understand both the temporal and spatial spread of CWD in our study areas. The knowledge gained from this study will be combined with the results of parallel investigations on dispersal, migration, and contact rates to develop a spatial model of chronic wasting disease spread in southern Saskatchewan.

CHAPTER 4
FACTORS INFLUENCING CONTACT BETWEEN MULE DEER (*ODOCOILEUS
HEMIONUS*) IN A CHRONIC WASTING DISEASE ENDEMIC ZONE IN
SASKATCHEWAN

4.1 Abstract

Although it is known that chronic wasting disease (CWD) can be spread through both direct and indirect contact, the role of each in the transmission and spread of CWD in free-ranging populations has yet to be defined. We investigated the effects of season and landscape on patterns of direct and indirect contact between GPS-collared mule deer from five study areas located in and around a CWD-endemic zone in southern Saskatchewan. Direct contacts were identified using proximity and indirect contact was measured using shared space use.

Overall probability of contact for GPS-collared deer was 0.092 ($n = 107$). Same-sex contacts were more common than between-sex contacts during all seasons, and all contact types were most likely to occur during the late winter and early spring (February-April). This finding agrees with the tendency of mule deer to aggregate into large groups during the late winter and suggests that this may be an important time period for CWD transmission. Direct contacts were found to occur more in cropland and wetland than expected based on availability, whereas they occurred less than expected in grassland. The opposite was true for indirect contact, which tended to occur more than expected in areas of low elevation and rugged terrain, and in grassland or shrub/wood habitats. These results suggest that cropland may be considered a high risk habitat for direct CWD transmission between individuals, and that rugged, low elevation areas such as

coulee bottoms may be high risk areas for environmental contamination and indirect transmission of CWD.

4.2 Introduction

Since the discovery of chronic wasting disease (CWD) in free-ranging deer populations in Saskatchewan, control of this disease has been a challenging task for management agencies in the province. Similar to many other CWD management programs across North America, hunter-based population reduction has been the primary strategy, with the goal of reducing population densities to levels low enough to stop disease spread. This program has been unsuccessful in preventing the spread of CWD to areas outside of the original management areas, and as of spring 2009, CWD had been found in thirteen wildlife management zones in the province (Saskatchewan Ministry of Environment 2009). One of the many factors hindering effective management of CWD is uncertainty regarding specific mechanisms of its transmission and spread among free-ranging populations (Bollinger et al. 2004, Wasserberg et al. 2009). Several researchers have addressed this question and models have been constructed attempting to fit prevalence data to a particular mode of transmission, but disagreement remains due to the complexities of environmental contamination, movements of individuals, and social structure within populations (Gross, Miller 2001, Schaubert, Woolf 2003, Wasserberg et al. 2009, Joly et al. 2006). The addition of quantitative, region-specific information regarding contact and social structure would be beneficial in continuing to improve models to guide and inform management decisions.

Contact within free-ranging populations of large, mobile animals is difficult to measure, particularly over large geographic areas. Several methods have been used to explore potential interactions between individuals, such as calculating the frequency at which an individual is

located within the home range of another individual or population unit (Conner, Miller 2004), measuring home range overlap (Millsbaugh et al. 2004, Atwood, Weeks 2003), and visually observing groups of individuals (Lingle 2003, Bowyer et al. 2001). Within the past decade, advances in technology have facilitated the use of proximity between individuals at a point in time as a rough measure of contact through the use of proximity collars, which log the occurrence of a contact event when two collared animals come within a particular distance of each other (Prange et al. 2006). This idea has also been applied using GPS (Global Positioning System) collars to measure proximity between collared individuals (Schauber et al. 2007, Kjær et al. 2008, Schuler 2006). As GPS collars automatically record locations at programmed intervals, potential contact events can be identified when simultaneous locations from two individuals are recorded within a threshold distance of each other. Proximity does not provide enough information to determine whether actual contact has occurred or whether sufficient contact has occurred for disease transmission, but it is reasonable to assume that probability of physical contact should increase as frequency of close proximity events increases between a pair of individuals. Although we recognize the limitations of using proximity as an index of contact, for ease of discussion, “close proximity events” will be hereafter referred to as “direct contact events”.

Due to the extreme resistance of prions to environmental degradation and the importance of indirect transmission as a mechanism of CWD spread, we must also consider factors affecting spatial distribution of infectious prions in the environment. Patterns of CWD spread through environmental contamination will likely be influenced by soil type and other factors leading to increased infectivity in the environment (Johnson et al. 2006, Schramm et al. 2006), but will also

depend upon patterns of spatial overlap between individuals, hereafter referred to as “indirect contact”.

The objectives of this study are to investigate the effects of sex, age, and season on probability of contact between GPS-collared mule deer in southern Saskatchewan, and to identify habitat and landscape characteristics that may be associated with increased risk of CWD transmission through direct or indirect contact. Although contact between individuals has been investigated in white-tailed and mule deer in other areas affected by chronic wasting disease, it is important to consider behavioural differences between species and populations occurring in different geographic regions subject to a unique set of environmental influences (Lingle 2003). Also, few studies of this type have addressed contact between both sexes of deer due to difficulties deploying GPS collars on males for extended periods of time (Kjær et al. 2008). Information regarding contact between male and female mule deer will provide insight into prevalence differences between the sexes, thought to be caused to some degree by behavioural differences (Miller, Conner 2005). Knowledge gained through this study will be used, along with results from the preceding chapter and collaborative studies, in the development of predictive models and strategies to manage the spread of CWD in Saskatchewan.

4.3 Methods

4.3.1 Study areas

This study was conducted in five study areas in southern Saskatchewan near the Saskatchewan Landing area of the South Saskatchewan River (Bounded by $-108^{\circ}27'$ and $51^{\circ}10'$ in the northwest and $-106^{\circ}12'$, $50^{\circ}25'$ in the southeast) (Figure 4.1). Four of the five sites fall within the Mixed Grassland Ecoregion of Saskatchewan, while the fifth, most north-easterly site falls within the Moist Mixed Grassland Ecoregion (Acton et al. 1998). The total area covered by

all study sites combined is equal to approximately 2700 km², with each site ranging from approximately 250 to 800 km².

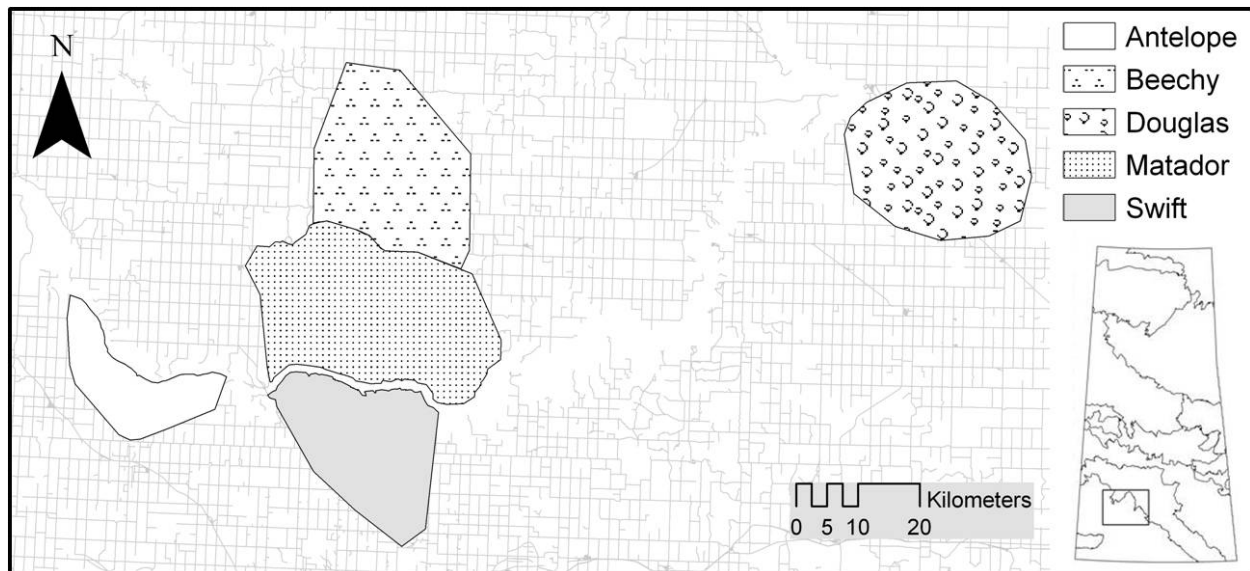


Figure 4.1. Locations of study sites in southern Saskatchewan.

The Mixed Grassland Ecoregion is characterized by a semiarid climate with mean annual precipitation of 352 mm, mean July temperature of 18.9°C and mean January temperature of -12.6°C (Acton et al. 1998). Annual cropland makes up a major proportion of the study sites, while the remaining habitat is composed mostly of mixed grass prairie across rolling pastureland and through the river valley and deciduous shrubs in coulees and low lying areas (Figure 4.2). Very little forest cover is present except in the Douglas study site, where patches of aspen forest (*Populus tremuloides*) and deciduous shrubs are dispersed among pasture and sand hills habitats. Common annual crops of this region are barley, durum, wheat, oats, canola, peas and lentils (Saskatchewan Ministry of Agriculture 2008). Please refer to general materials and methods for a more detailed description of the study sites.

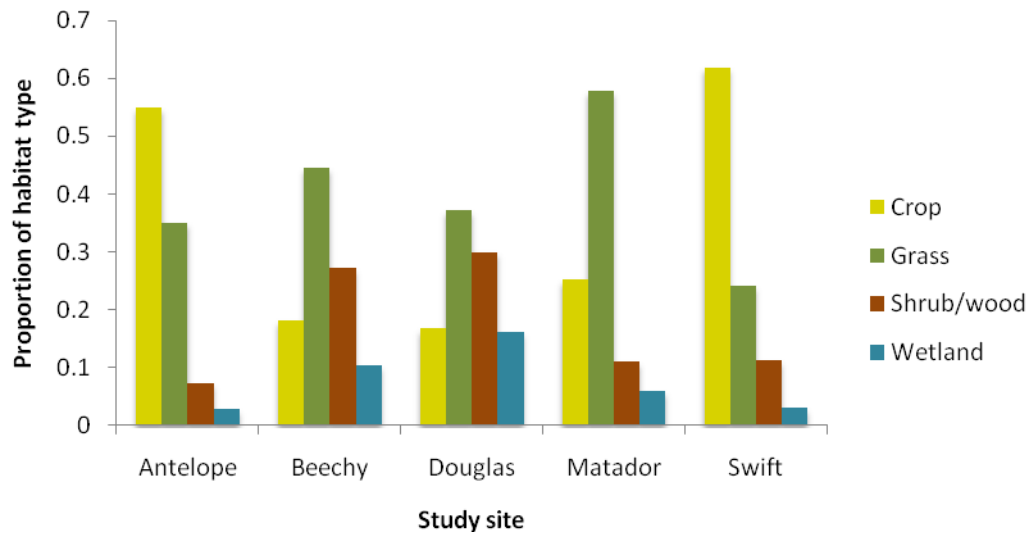


Figure 4.2. Proportional contribution of generalized habitat types to each study area.

4.3.2 Capture and collaring

Deer were captured between January and April of 2007 and 2008 using either modified clover traps (Clover 1956, McCullough 1975) or a helicopter and net gun (Barrett et al. 1982). All deer were chemically immobilized with intramuscular injections of a combination of Telazol® and Xylazine (Rompun®) and reversed with Atipamezole (Antisedan®) after collar deployment and sample collection. Animal handling protocol was approved by the Animal Care and Use Committee. Each deer was fitted with a GPS collar (LOTEK, Televilt) programmed to take automatic fixes every 1-6 hours. Male collars were fitted with specially designed foam inserts to allow for neck swelling during the rut. All GPS-collared deer were tracked monthly to identify long distance movements and to periodically download data from collars equipped for remote communication. Collars were retrieved during February and March of 2009. GPS fixes

taken at 4, 8, 12, 16, 20, and 24 hours were used for this analysis, excluding erroneous or suspect data points and data occurring within the first two weeks of initial capture.

4.3.3 Identifying direct contact events

Contact events were identified using the “proximity” tool in ArcGIS 9.2 (ESRI 2007) with a set threshold distance of 25 m. This threshold distance was chosen to account for collar error. All simultaneous locations from two different deer occurring within the threshold distance of one another were selected as direct contacts. Location pairs for each contact event were then linked by vectors using Crime Analysis Spatial Extension (CASE) (Crime Mapping and Analysis Program 2005) for ArcGIS. A buffer with a radius of 12.5 m was drawn around each contact vector to create a polygon encompassing both locations of a contact event while allowing for location error. Contact polygons were overlaid on a 25 m resolution habitat map of the study area as well as a digital elevation model (DEM) (Government of Canada, Centre for Topographic Information 2000-2009) and a terrain ruggedness layer (TRI) calculated from the DEM using a topographic ruggedness script (Evans 2004). The habitat map was created by classifying SPOT (System Pour l'Observation de la Terre) multispectral imagery (Alberta Terrestrial Imaging Centre 2007) (See section 2.4.1 for a detailed description of image processing). Habitat proportions, average elevation, and average ruggedness values were calculated for each of the contact polygons, and values were averaged for each deer pair.

Non-independent pairs of deer were identified using a Coefficient of Association calculation (Cole 1949). Using this measure, deer were identified as part of the same social group if greater than 50% of their simultaneous locations were within 100 m of each other. Because mule deer in this area tend to have relatively fluid social group structure, only four deer pairs in the dataset met these criteria. To avoid bias in the analysis, one dataset was chosen

randomly for analysis in all cases where both non-independent deer were involved in contacts with another individual.

4.3.4 Identifying shared use areas

To calculate areas of shared use, kernel home range rasters (See section 2.4.3) for both deer were multiplied together to create a new raster of joint utilization distribution (JUD), or joint space use, where each cell is the product of the utilization distribution (UD) values of the two overlying cells (Schauber et al. 2007, Millspaugh et al. 2004) (Figure 4.3). Using this method, high intensity of use by both deer in a particular area results in high UD values, which in turn, result in high joint utilization distribution values for that area. Low JUD values result from low intensity of use by both deer or from high intensity of use by only one individual of the pair. Ten concentric contours were then calculated to delineate areas containing decreasing values of joint use (Figure 4.3d). We modified methods used by Kjør et al. (2008) to derive habitat proportions and average ruggedness and elevation weighted by intensity of use by both deer. Using these methods, raw habitat proportions and averages were calculated for each contour and multiplied that contour's average joint use value. The calculations for each contour were then summed and divided by the sum of all average joint use values. Habitat proportions within polygons with greater shared use received more weight than proportions within polygons of low shared use. Without accounting for intensity of use by both deer of a deer pair, there is the potential to make inaccurate conclusions about high likelihood of direct contact in certain habitats simply because they are favorable habitats frequented by both deer (Kjør et al. 2008).

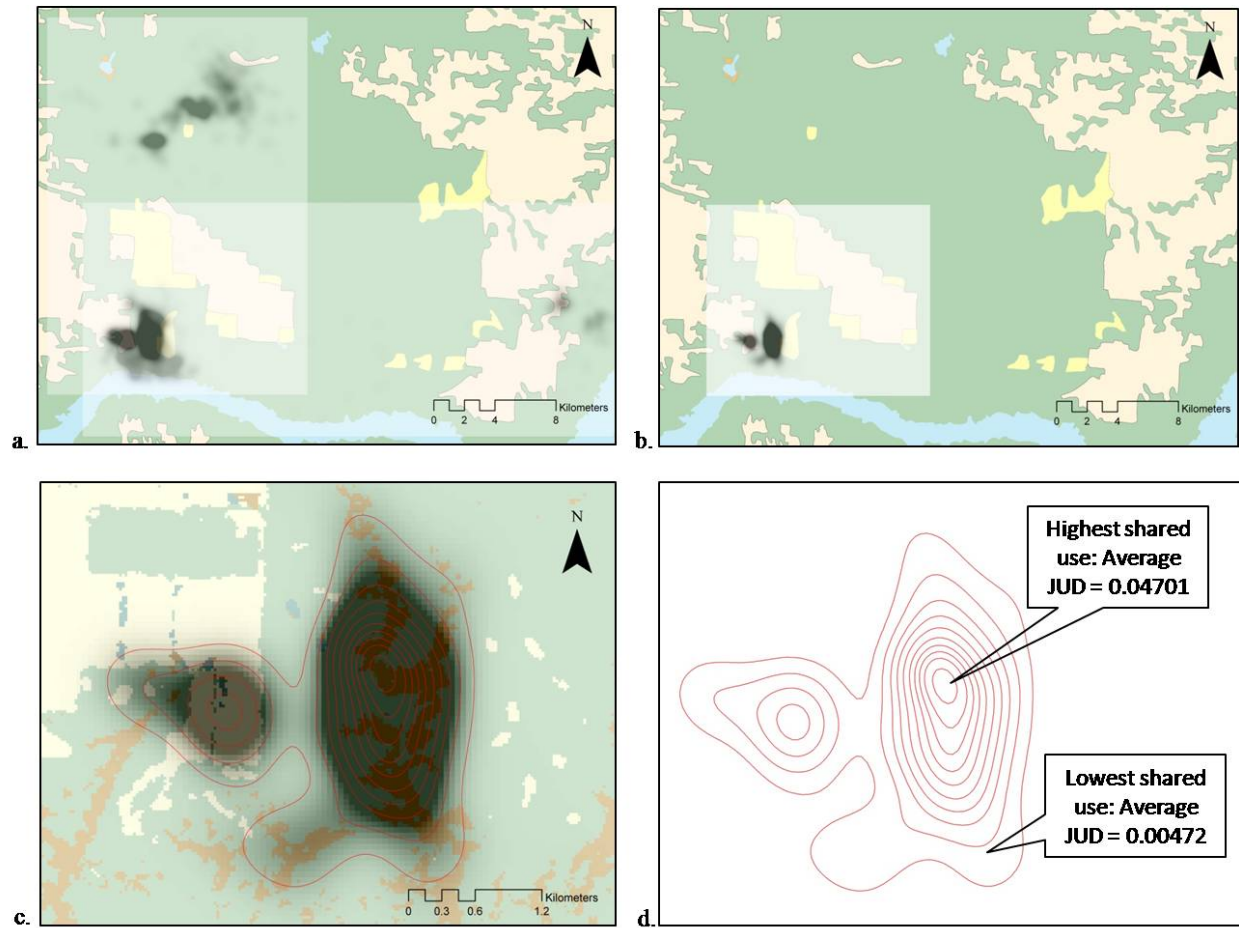


Figure 4.3. Individual home range rasters multiplied together (a) to calculate a raster of shared use (b) where each cell represents a joint utilization distribution (JUD) value that is higher with increasing shared use (c). Concentric contours delineate areas of decreasing shared use (d) and habitat proportions are calculated within each contour and weighted by the corresponding average JUD value.

4.3.5 Analysis

4.3.5.1 Temporal analysis of direct contact

Analysis of contact rates was conducted from the viewpoint of the individual deer, where each GPS location for each deer was classified as “contact” or “non-contact”. Using individual deer as the sampling unit allowed us to calculate actual contact rates between all radio-collared deer, accounting for deer that did not contact any other deer as well as the total number of non-

contact locations for each deer. Contact locations were further classified as same-sex or between-sex and same-age or between-age. SAS 9.1 (SAS Institute 2002) was used to perform logistic regression adjusted for repeated measures for each deer. We investigated the effects of study site, year, sex, and season on contact rates, as well as interactions between any of these factors. Our sample size of juvenile deer was insufficient to properly investigate interactions between age and other significant factors. To ensure that our results were not biased, we ran all tests with juveniles removed to determine whether results would still be significant in the absence of juvenile contact data. Contact rates were also analyzed by month to test for statistically appropriate seasonal divisions, which were then accepted based on their significance to mule deer biology and behaviour. Seasonal categories were as follows: Season 1 = February-April (winter, gestation); 2 = May-July (spring, pre-parturition, fawning, nursing); 3 = August-October (summer, pre-rut); 4 = November-January (fall, rut).

4.3.5.2 Spatial analysis of direct contact

A hierarchical resource selection approach was adopted for habitat analysis. All deer pairs contacting each other ten or more times were chosen for habitat analysis. After exclusion of four pairs to maintain independence, the total number of deer pairs used for analysis was 101. Each deer pair was classified by sex as male-male, female-female, or male-female, as well as by age as adult-adult, juvenile-juvenile, or adult-juvenile. Average habitat proportions and terrain ruggedness and elevation values calculated for contact events of each deer pair were designated as “used” landscape values, while weighted values calculated for each jointly used area were set as “available” (Kjær et al. 2008). Mixed model linear regression was performed in SAS 9.1 to compare used and available habitat and landscape values while adjusting for deer pair and site.

4.3.5.3 Spatial analysis of indirect contact

The next level of habitat selection analysis was to determine whether pairs of deer tend to share particular habitat types more than expected based on available habitats found within their independent home ranges. For this analysis, used habitat proportions and ruggedness and elevation values were calculated for the 95% contour of each deer pair's shared area. Available habitat and topographic values were calculated within each individual's home range and averaged across both home ranges, weighted by the relative size contribution of each home range. Mixed model linear regression was again performed to compare used and available habitat proportions and ruggedness and elevation values.

4.4 Results

4.4.1 Dataset

A total of 107 deer were used in this analysis (49 ADM, 34 ADF, 11 JVM, and 13 JVF). Of these deer, 81 were captured in 2007 and 26 were captured in 2008. Numbers of deer collared in each study area were not equal (Antelope = 31, Beechy = 8, Douglas = 16, Matador = 26, and Swift = 26), nor was the distribution of collars within each area. The total number of locations collected for each deer ranged from 6 to 4361. Of these deer, 94 individuals were involved in at least one contact with another individual. The average number of contacts per deer was 202 (SE = 33.7) and the average number of contact partners per deer was 5.1 (SE = 0.389) (Table 4.1).

Table 4.1. Summary of contacting deer, average contacts per individual, average contact probability (contacts/ total number of locations) and average number of partners per individual.

Age/sex class	Total individuals	Deer contacting others	Proportion of deer contacting others	Average contacts per individual	Average contact probability	Average partners per individual
Overall	107	94	0.88	202	0.092	5.1
Adult male	49	45	0.92	237	0.072	5.8
Adult female	34	28	0.82	215	0.100	4.4
Juv male	11	10	0.91	71	0.144	4.3
Juv female	13	11	0.85	145	0.077	4.9

4.4.2 Effects of sex, age, and season on contact rates

The overall probability of contact between GPS-collared mule deer in our study areas was 0.092 (CI: 0.063 – 0.121), with no significant differences between males and females ($\chi_1^2 = 0.10$, $p = 0.750$) or adults and juveniles ($\chi_1^2 = 2.51$, $p = 0.113$). There were differences between study sites ($\chi_4^2 = 19.0$, $p < 0.001$) with Swift having the highest probability of contact at 0.18 (CI: 0.12 – 0.26) and Douglas having the lowest at 0.007 (CI: 0.004 – 0.015) (Figure 4.4). However, inferences cannot be made based on these values because of the many confounding factors that could be responsible for study site differences, such as differences in collar distribution in and proportion of deer collared among study areas. The same can be said for differences between sex and age classes.

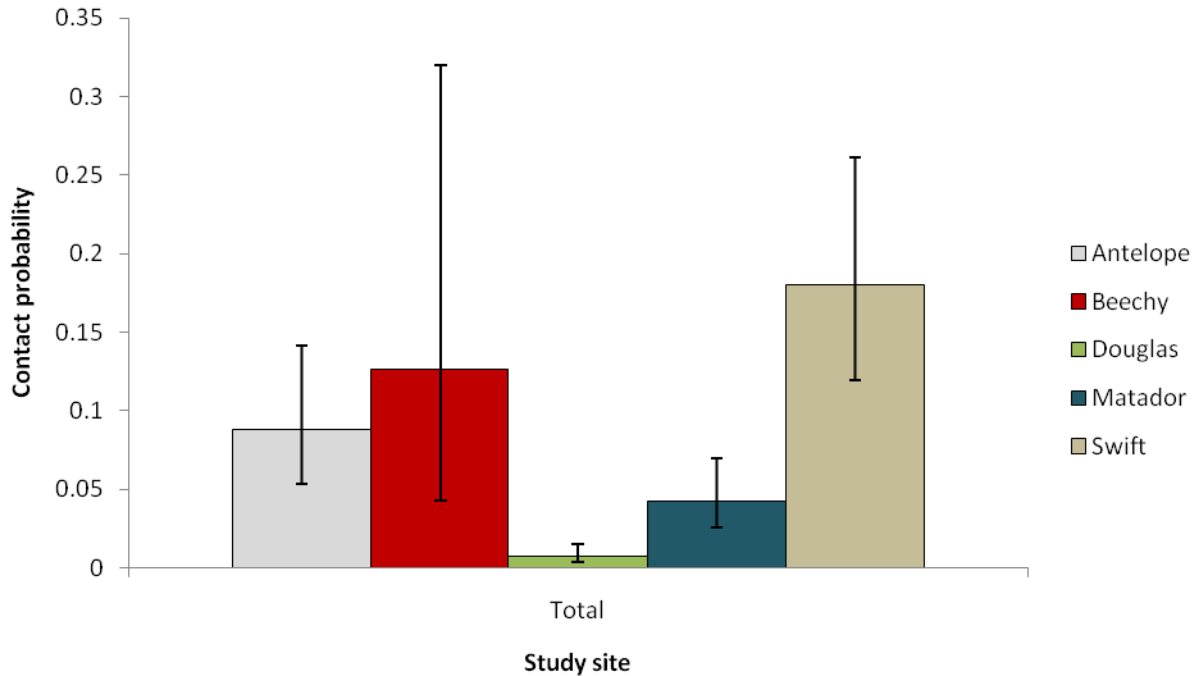


Figure 4.4. Differences in contact probabilities between study sites ($\chi^2_4 = 19.04$, $p < 0.001$) (Error bars are 95% confidence intervals). Overall contact probability for all study areas was 0.092 (CI: 0.063 – 0.121).

Probability of contact varied between all seasons ($\chi^2_3 = 28.5$, $p < 0.001$), as was expected based on literature and field observations, with contacts being three times more likely during season 1 (Feb-Apr) than season 2 (May-Jul) and at least 2.6 times more likely than contacts in seasons 3 and 4 (All $p < 0.001$). Although we did not detect differences in overall contact probability between males and females, seasonal trends in contact likelihood differed between sexes (Figure 4.5). Both males and females were equally likely to contact other collared deer during season 1 when contact rates were highest ($p = 0.756$) and during season 3 ($p = 0.783$), but during season 2, males were 2.7 times more likely than females to contact other individuals ($p = 0.038$). The opposite was true for season 4, when the likelihood of female deer contacting other individuals were 2.5 times greater than the likelihood of males contacting other deer ($p = 0.024$).

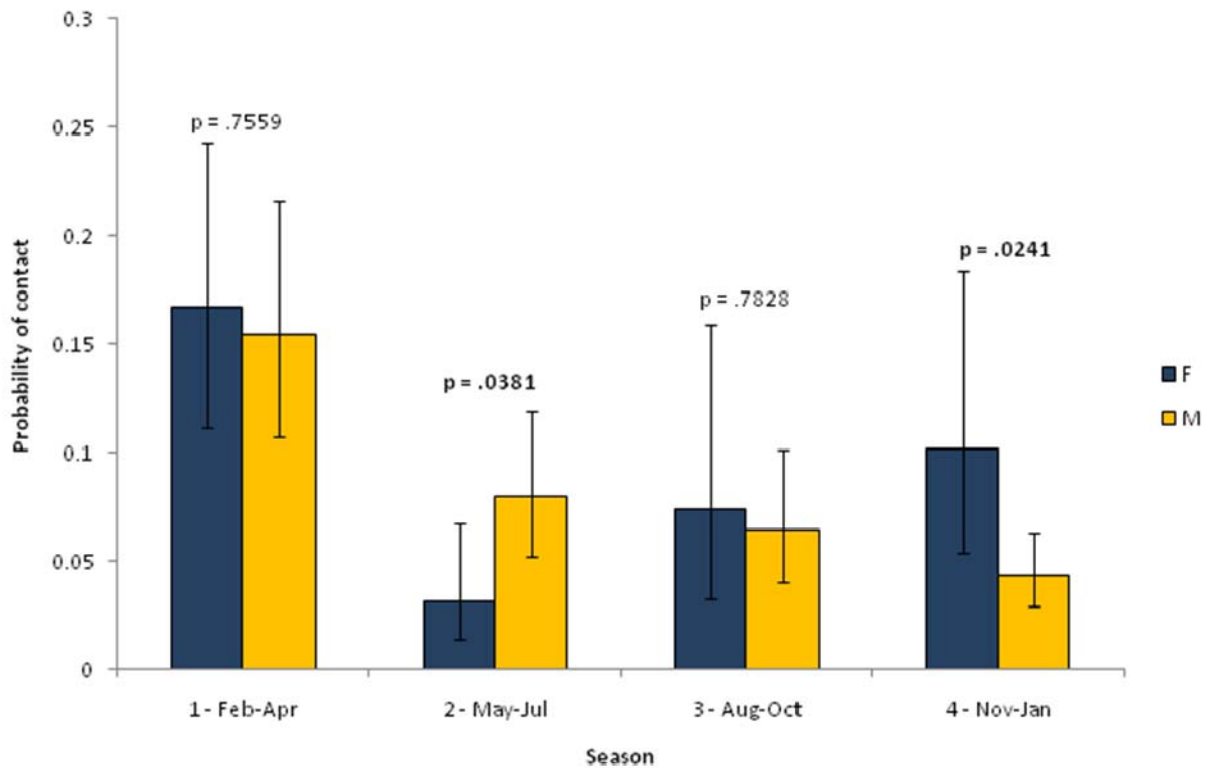


Figure 4.5. Seasonal differences in contact rates between males and females. Error bars are 95% confidence intervals.

We also tested the probability, in the event that a contact occurred, whether the individuals involved would be of the same or opposite sex. Probability of same-sex contact vs. between-sex contact was not affected by study site ($p = 0.474$), age class ($p = 0.768$) or sex class of contacting individuals ($p = 0.060$), but season was a significant factor ($\chi^2_3 = 11.2$, $p = 0.011$) as was the interaction between season and sex ($\chi^2_3 = 9.43$, $p = 0.024$). Contacts were more likely to occur between individuals of the same sex during all seasons of the year, but the probability of between-sex contacts was lowest during season 3 at 0.294 (CI: 0.224 – 0.376) and highest during season 4 at 0.387 (CI: 0.302 – 0.478). This trend remained true for males when we explored the

interaction between season and sex, but there were no significant differences in the probability of between-sex contacts between months for females.

The investigation of whether contacts were more likely to occur between individuals of the same age class did not return any conclusive results. The probability of same-age contacts vs. between-age contacts did not differ by season, sex, age, or time of day. However, this could be due to our small juvenile sample size and should be viewed with caution.

4.4.3 Habitat and landscape factors influencing direct contact

For this analysis, deer pair was used as the study unit and pairs were selected that contacted each other more than 10 times. In the cases where a pair of deer was found to be non-independent ($n = 4$ pairs) and a third individual was found to contact both members of the pair, one of the pairs involving the third individual was randomly excluded from the analysis. Of a total of 274 contacting deer pairs, 101 pairs were used in the analysis, with 121.3 contacts per pair on average ($SE = 20.8$).

Direct contacts tended to occur in agricultural land ($F_{1,100} = 43.9$, $p < 0.001$) and wetland ($F_{1,100} = 3.96$, $p = 0.049$) more than expected based on availability (Figure 4.6). The opposite was true for grassland, where the proportion found in areas shared by deer pairs was higher than in areas associated with contact events ($F_{1,100} = 41.04$, $p < 0.001$). Contacts occurred at higher elevations than expected ($F_{1,100} = 4.71$, $p = 0.032$), but there were no differences between amount of shrub land in areas associated with contact events when compared to areas commonly used by deer pairs ($p = 0.537$), nor were there differences in ruggedness ($p = 0.370$). Age and sex structure of the deer pair did not influence whether or not contacts were associated with these habitat types or landscape characteristics.

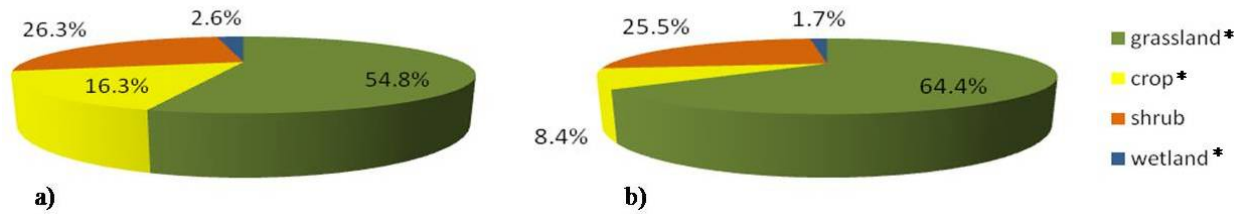


Figure 4.6. Differences between habitat proportions associated with direct contact events (a) and those associated with shared use areas (b). Stars indicate significant differences.

4.4.4 Habitats and landscape factors influencing indirect contact

When we looked at habitats and landscape characteristics associated with areas of indirect contact, we encountered different results than with direct contact. Indirect contact tended to be associated with grassland ($F_{1,100} = 85.62$, $p < 0.001$) and shrub/woodland ($F_{1,100} = 25.3$, $p < 0.001$) when compared with areas available to each deer (Figure 4.7). In contrast, areas jointly used by pairs of deer contained less cropland ($F_{1,100} = 51.41$, $p < 0.001$) and wetland ($F_{1,100} = 172.0$, $p < 0.001$) than expected based on availability. Female deer pairs used wetland habitats more in general than mixed-sex and male deer pairs ($F_{2,100} = 6.81$, $p = 0.002$), but there was no interaction between sex, indirect contact and wetland. Commonly used areas also tended to be more rugged ($F_{1,100} = 111.1$, $p < 0.001$) and occurred at lower elevations ($F_{1,100} = 4.53$, $p = 0.036$) than individual home ranges. Juvenile deer pairs tended to make more use of rugged terrain ($F_{2,100} = 8.64$, $p = 0.003$), but age class did not affect the relationship between indirect contact and topography.

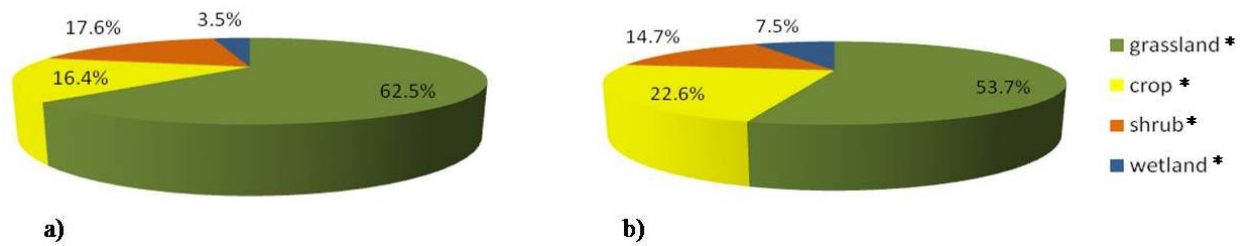


Figure 4.7. Differences between habitat proportions found in areas of indirect contact (a) and those measured within individual home ranges (b). Stars indicate significant differences.

4.5 Discussion

4.5.1 Temporal changes in contact rates

This study allowed us to quantify the effects of ecological and biological factors on direct contact between collared mule deer. Because of potential confounding factors and unknowns related to proportion and distribution of collared deer in our study population, we are unable to extrapolate rates of contact to the entire deer population, or accurately measure differences between male and female contact rates or between study sites. It can be assumed that actual contact rates between mule deer would be higher than those between collared deer, but in situations where two deer were captured in the same trap, the probability of contact between those individuals may be higher. We can also assume that contact between collared deer would be related to group size, as probability of two collared deer being in the same group would increase as group size increases. Despite the limitations of methods used in this study, the observed changes in contact probabilities among male and female GPS-collared deer in response to season can be applied to the overall population of mule deer in our study areas.

An interesting finding is that contact rates in general were relatively low during season 4 (November - January). We would expect that contacts, particularly between-sex contacts would increase during season 4 due to the breeding season, which occurs during this time period in our

study areas. Although we did see the highest probability of between-sex contacts during this time, same-sex contacts were still more likely, and overall contact rates during this time were much lower than during season 1. Breeding behaviour has been suggested as an explanation for observed higher CWD prevalence in males of both mule and white-tailed deer as behaviours such as sparring, visiting scrape sites, and attempting to mate with many females could result in greater disease exposure among males (Miller, Conner 2005, Gear et al. 2006). Although breeding behaviour likely plays an important role in disease transmission, our results showed that the late winter/early spring, rather than the breeding season, was the most likely time for direct contacts to occur for both males and females. These findings agree with field observations as well as published literature reporting the tendency of mule deer to form large mixed-sex groups during the late winter months (Wood et al. 1989, Lingle 2003), but differ from studies of mule deer in different geographic regions, which report greater aggregations during the rut than any other season (Bowyer et al. 2001).

The low incidence of between-sex contacts in our study areas during the rut could be explained by mule deer breeding behaviour, where a male will tend a single female for a period of time until breeding occurs (Geist 1981). Depending how long this tending period continues, and how close the female allows the male to approach, it is possible that few direct contacts would be identified using the methods of this study. Despite these relatively low direct contact rates, the breeding season should not be dismissed when considering patterns of disease transmission in mule deer. For example, an important part of tending behaviour is female urination to signal receptiveness to breeding, after which the male will investigate and assess the urine (Estes 1972, Kucera 1978). Because infectious prions have been found in the urine of

infected deer (Haley et al. 2009), this behaviour, among other breeding-related behaviours, could serve as an important mode of indirect CWD transmission in mule deer (Miller, Conner 2005).

4.5.2 Factors affecting spatial distribution of contact events

Relationships between particular habitat types and direct contact by mule deer can be attributed to a combination of resource availability and predation risk. Mule deer are reported to aggregate in open areas away from escape cover, a behaviour thought to have evolved in response to predation risk (Bowyer et al. 2001). Although the majority of direct contacts recorded in this study took place in grassland habitat, the habitat selection approach revealed that this habitat type, which is dominant throughout three of the five study sites, is actually less likely to be associated with direct contacts than expected based on its shared use by deer pairs, whereas cropland and wetland tended to be associated with direct contacts.

Wetlands provide concentrated sources of water and succulent forage, particularly during the late summer months when ephemeral wetlands have dried up and few water sources remain. Vulnerability to predation while visiting water sources may explain why direct contacts occurred in this habitat type more than expected. These results suggest that wetlands may create opportunities for direct CWD transmission as well as point sources of environmental contamination with infectious prions. Cropland also provides semi-concentrated sources of high-quality food during the growing season and harvest (Kjær et al. 2008), but also during the winter when mule deer are seen, though less often than white-tailed deer, feeding on crop residue or standing hay (Wood et al. 1989). Although food sources of this type are spread over relatively large areas, it may be more beneficial for individuals to feed in close proximity to each other to protect against predation (Lingle 2003, Bowyer et al. 2001). In contrast to cropland, grassland habitats in these study areas are often associated with rough topography and made up of a more

patchy landscape composition. Like cropland, grassland is a relatively open habitat, but patches of shrub and other food sources as well as escape terrain are more diffuse and readily available than on cropland, so it may be less necessary for deer occupying grassland habitats to associate with other individuals in order to take advantage of resources or to avoid predation.

4.5.3 Factors affecting shared space use

Indirect contact between pairs of deer was investigated by calculating areas of shared use by both deer, as well as the intensity of use by both deer (Schauber et al. 2007, Millspaugh et al. 2004). Comparing habitats within these areas with habitats available to each member of the deer pair allows us to identify habitats and landscape features that may lead to certain areas being frequented by multiple deer, at the same or at different times. This portion of the investigation has implications for the transmission of chronic wasting disease and any disease of mule deer whose agent can be shed and remain infectious in the environment. Although we know little about the dynamics of indirect transmission of CWD, we do know that prions are highly resistant to degradation and can remain infectious in the environment for years (Miller et al. 2004). Although there are other factors like soil type, which are likely to influence patterns of environmental CWD transmission (Johnson et al. 2006, Schramm et al. 2006), we can assume that the probability of environmental contamination and subsequent transmission to susceptible deer should increase as intensity of shared use by multiple deer increases.

Our results showed that indirect contact in our study areas was associated with rugged topography and grassland and shrub/wood habitats, but not with crop or wetland. These results differ from those seen in our investigation of habitat relationships with direct contact, but can be explained by behavioural and habitat use patterns. As mentioned previously, although cropland provides a seasonal, high quality food source, it does not provide a suitable year-round habitat

for mule deer and provides little protection from predators and the elements (Wood et al. 1989). It stands to reason that areas of cropland are not commonly shared by multiple deer, but when they are it is most often by groups of deer taking advantage of a food source at a particular time while grouped close together to minimize vulnerability to threats.

The associations between indirect contact and both shrub/wood habitat and rugged terrain are particularly important for the potential spread of chronic wasting disease. In an area dominated by agriculture and open grassland habitat, small patches of shrub and woodland provide important sources of escape cover and forage, which leads to their shared use by many deer (Wood et al. 1989). Although this habitat is commonly shared, the protection provided by vegetative cover likely allows for solitary feeding and bedding leading to lower than expected rates of direct contact. The same can be said for areas of rugged terrain, where mule deer occupying hill tops or sides of cliffs have an advantage over predators (Lingle 2003). Rates of direct contact did not differ from expected in high ruggedness areas, but risk of indirect contact was found to be high. The importance of rugged terrain in mule deer habitat results in higher deer concentrations and greater spatial overlap between individuals occupying the rugged networks of drainage features found in our study areas. Despite the lower risk of direct contact associated with these habitat types, our results suggest that coulees, creek valleys and other rugged topographic features, as well as patches of shrub and woodland in our study areas may be important sources of environmental contamination and indirect CWD transmission between mule deer.

4.6 Conclusion and management implications

As chronic wasting disease is known to be transmitted through both direct and indirect contact, it is important to consider both aspects of disease transmission in attempting to

understand or predict patterns of disease spread. We used proximity as a means to quantify direct contact between pairs of mule deer and shared space use as a measure of indirect contact.

Although these techniques limit the amount of information that can be obtained regarding type and duration of contacts (Kjær et al. 2008), they allow us to understand social patterns between mule deer of both sexes, and how these patterns are influenced by habitat and season. Further research should build on these results by determining the type and intensity of contacts occurring between deer in these habitats and how each may contribute to CWD transmission. This could be carried out by direct observations, or through the use of trail cameras or video cameras distributed across various habitat types to collect fine-scale information on contact rates.

Our observations and results suggest a fluid social structure for both males and females, agreeing with results of a study in California, where group composition tended to be unstable, changing with diurnal peaks of activity (Bowyer et al. 2001). Observed seasonal changes in contact rates highlight the importance of late winter/early spring grouping behaviour as a potential transmission mechanism for all age/sex classes. Low contact rates reported during the rut do not dismiss the importance of this time period in disease transmission, but rather emphasize the need for further investigation to better understand how different aspects of breeding-related behaviour contribute to both direct and indirect transmission of chronic wasting disease.

The identification of particular habitat types associated with higher risk of direct or indirect CWD transmission can benefit managers by allowing them to focus their efforts toward specific areas or to apply varying levels and types of management to different habitat types. Increased indirect shared space use by deer in rugged terrain and shrub/woodland suggests that these habitat types are at higher risk for environmental contamination in areas affected with

CWD. In the event that feasible techniques are developed to detect the presence of infective prions in soil, researchers could improve their chances of identifying contaminated areas by targeting these habitat types. Higher risk of direct contact between deer in cropland suggests that farm management practices may aid in disease management through reducing deer use of agricultural land during particular seasons. Alfalfa hayfields and annual legume crops such as peas and lentils are attractive to mule deer during the mid to late summer, and hay bales, grain piles and silage are likely to draw aggregations of deer during the winter season. Use of fencing to keep deer away from resource sites and planting unpalatable crops in areas of high deer use may help to manage the spread of CWD in affected areas. Further research investigating mule deer use of specific crop types, as well as the use of supplemental resource sites would add to this study and aid in developing recommendations for landowners and managers.

Quantitative information regarding contact patterns of mule deer will complement parallel studies investigating relationships between landscape and coarser-scale movement patterns like home range size, migration and dispersal. Knowledge such as this will help researchers and managers gain insight into observed prevalence differences between male and female hosts, as well as recognize similarities and distinctions between different geographic regions affected by the disease. Predictive models of CWD spread can benefit from data showing seasonal changes in contact rates, as well as the identification of landscape and habitat characteristics that may be associated with higher direct or indirect transmission risk. This will in turn aid in the development of better management strategies and open up new avenues of research that will help bring researchers closer to fully understanding the dynamics of chronic wasting disease spread.

CHAPTER 5 GENERAL DISCUSSION

5.1 Introduction

In 2001, a management plan was implemented in Saskatchewan in response to the discovery of a hunter-shot mule deer infected with chronic wasting disease in the western region of the province. The main objective of this plan was to reduce deer numbers in and around the affected area in order to slow transmission and eventually eradicate the disease. Due to a number of reasons that may include difficulties reaching and maintaining target population densities, short duration of the program, potential spillover events from infected cervid farms, and long-term environmental persistence of the disease agent, CWD was not eradicated from the province. The number of regions within the province affected by the disease began to increase, including areas far from the initial infection and in the neighboring province of Alberta (Kahn et al. 2004, Wilson et al. 2009). Similar outcomes have occurred in the United States where wildlife managers have attempted to control the spread of CWD in wild deer and elk populations, for decades in some states (Spraker et al. 1997, Williams, Miller 2002, Williams et al. 2002a).

Collaborations between researchers and management agencies across North America have resulted in a rapidly expanding knowledge base surrounding this relatively new prion disease. It is generally agreed that once the disease becomes established in a wild population, eradication is unlikely and would require maintenance of host populations at very low densities for extended periods of time (Williams et al. 2002b, Miller et al. 2006, Gross, Miller 2001). These goals are extremely difficult to attain, due to the expensive and controversial nature of

such programs (Needham et al. 2004, Williams et al. 2002a), as well as the unknown duration over which population densities must be managed (Miller et al. 2006). The most promising courses of action are early detection and prevention of spread into uninfected areas (Pybus, Hwang 2008); however, early detection is difficult and expensive as well and depends on the ability to obtain sufficient sample sizes (Blanchong et al. 2008). Success will be aided by a greater understanding of CWD transmission mechanisms (Wasserberg et al. 2009, Miller et al. 2006), novel techniques to facilitate the detection of prions in the environment (Conner et al. 2008), and the development of accurate models that will predict patterns of CWD spread across the landscape, allowing researchers and managers to identify areas at risk and implement appropriate prevention strategies (Blanchong et al. 2008). Predictive models require information on disease dynamics, but also baseline biological and ecological information relevant to the population in question, such as rates of contact and dispersal, as well as home range size and relationships between these movement patterns and the surrounding environment.

5.2 Research summary

5.2.1 Objectives

To address the need for quantitative movement information specific to deer populations in Saskatchewan, a long-term research project was undertaken in 2006 to investigate movement patterns of white-tailed and mule deer in five study areas of southern Saskatchewan and to identify environmental factors that influence these patterns. This thesis covered a portion of this project, in which home range sizes and contact patterns of male and female mule deer were investigated in relation to factors such as habitat, topography, and landscape heterogeneity. Specifically, this research:

- Provided accurate, quantitative information on male and female home ranges of mule deer in southern Saskatchewan and identified how landscape composition may affect home range size, and in turn, potential for CWD spread.
- Employed recently-developed methods to investigate the temporal and spatial distribution of direct contacts between deer in our study areas and identify particular seasons and habitats associated with higher risk of direct CWD transmission.
- Expanded these methods to identify habitats and landscape features that may be linked to increased risk of indirect transmission of CWD through environmental exposure.

5.2.2 Results and management implications

The first part of this project was initiated in order to fill an information gap on home ranges of mule deer in Saskatchewan. Although many studies have investigated home ranges of mule deer and their influencing factors, little information exists specifically regarding home ranges of mule deer in prairie environments (Wood et al. 1989), and virtually none is available for mule deer in this region of Saskatchewan. Individuals in our study areas expressed a wide variety of movement patterns, with a proportion of the population being seasonal migrators, others remaining relatively sedentary, and still others occupying large, sprawling home ranges or embarking on sudden, long-distance excursions. Other studies on mule deer movement have seen similar variation in movement patterns among individuals (Conner, Miller 2004, Wood et al. 1989, Sawyer et al. 2005). This variation led to difficulties in selecting methods for calculating home ranges, as some methods were appropriate for certain types of home ranges, but not for others. The methods chosen were suitable for our purposes, as they provided accurate estimates of the areas regularly traversed by individuals. However, they did not capture large areas of land covered briefly by migrating or dispersing individuals. Although long distance movements will

be addressed in a related study, home range sizes calculated using minimum convex polygons were included for supplementary information.

Males occupied larger home ranges than females, agreeing with the majority of published literature (Robinette 1966, Relyea et al. 2000). Home ranges also varied between study sites, with the largest sizes occurring in the Beechy and Matador sites, and the smallest occurring in Swift. Variation between sites was initially thought to be due to differences in the amount of continuous natural habitat available. Beechy and Matador are essentially composed of one large expanse of rolling pastureland (including the Beechy and Matador Community Pastures) that extends northward from the South Saskatchewan River. Road access is poor in the pasture and much of the area is not often disturbed by humans. Deer in these areas occupy large home ranges, often migrating seasonally between the two sites. The Swift and Antelope study sites contrast with the Beechy and Matador sites in that they consist of concentrated areas of natural habitat in the form of rugged creek valleys and networks of coulees surrounded by developed agricultural land. It was thought that deer in these areas may be much more limited by available natural habitat, occupying smaller home ranges within the creek valley and avoiding the surrounding cropland; however, additional analysis suggested that topographic ruggedness was more important than available natural habitat in determining mule deer home range size.

Mule deer are known to depend upon areas of rugged terrain for both predator avoidance and resource procurement (Lingle 2002, Wood et al. 1989, Lingle 2003). This explains the relationship between smaller home ranges and higher ruggedness values, as deer occupying rugged land may be able to meet their needs within smaller areas. Although smaller home ranges may decrease the rate of CWD spread outward from these areas, they result in greater intensity of use by individual deer, which may lead to more concentrated sites of environmental

contamination in areas occupied by CWD-positive deer. Rugged terrain was also found to be significantly associated with indirect contact between pairs of deer. Coulees and other topographic features associated with low elevation and shrubby vegetation are used by many deer for feeding, bedding, and as corridors through which to travel without increasing their vulnerability to predation. These patches of habitat make up a small proportion of the landscape in our study areas, but contain high deer densities relative to the surrounding environment and a large degree of spatial overlap between deer. Because of this, areas of rugged terrain, particularly those associated with vegetative cover, may be considered high risk areas for environmental contamination and indirect transmission of CWD. In the event that a cost-effective detection technique is developed to identify infective prions in soil, management agencies may benefit by focusing their efforts in coulee bottoms and other rugged landscape features with greater potential for environmental contamination.

This study also identified important relationships between cropland and deer behaviour that may be important in influencing CWD spread within deer populations. Despite its unsuitability for year-round deer habitat, individuals often feed on standing crops during the late summer and fall, and crop remnants or bales during the winter, when high quality food is scarce. The lack of protective cover and escape terrain in areas of cropland may explain probabilities of direct contact being higher than expected within this habitat type. Groups of deer tend to feed in close proximity to one another in areas with less available cover in order to decrease the need for individual vigilance and the overall vulnerability of the group (Lingle 2003, Bowyer et al. 2002). Group feeding increases the risk of disease spread between individuals through greater potential for direct contact and contamination of the food source with a disease agent. For this reason, cropland may be considered a higher risk habitat for transmission of chronic wasting disease.

Further research is necessary to identify seasonal relationships between mule deer contact and specific crop types, but CWD management may benefit by incorporating farming practices directed toward reducing mule deer use of agricultural land.

5.3 Limitations and future directions

The methods used in Chapter 4 to measure association between deer are valuable in understanding social structure and seasonal changes in grouping behaviour, both of which hold major implications for disease spread. However, the use of proximity as a measure of contact does not provide any information regarding the type and duration of contact occurring. Furthermore, these methods allow us only to investigate contact among radio-collared deer. Because of this, probability of contact will depend largely on the proportion and distribution of collared deer in the population. As we do not have accurate estimates of mule deer population density in our study areas, results of this study cannot be extrapolated to the overall population, nor can they be used to make comparisons between study areas or age/sex classes. Future research should build on these results by using visual observations to investigate contact patterns between collared and non-collared deer and further understand how specific types of contact and social behaviour may contribute to disease spread. In addition, spatial patterns of contact could be investigated further using motion-sensitive video cameras distributed throughout different habitat types to identify differences in fine-scale contact patterns.

Another limitation of the overall study was the small sample size of GPS-collared juvenile deer. The necessity for a two-year battery life resulted in the majority of GPS collars being too heavy for deployment on juveniles. A subset of smaller, lightweight drop-off collars (Televilt) were intended solely for use on juveniles, but these collars reached a failure rate of nearly 100% by the end of the second year and many were not recovered. Due to the small

sample size of the remaining GPS-collared juveniles, we were unable to test for differences between adult and juvenile contact rates. Although there were more VHF-collared juvenile deer available for home range analysis, only the first year of data could be used in the calculation of a juvenile home range (after which the individual would be considered an adult), resulting in an insufficient number of points to calculate an accurate kernel home range.

The management strategies that have typically been employed in attempts to control the spread of chronic wasting disease within and outward from affected areas include herd reduction as their central focus. Although this thesis investigated movement patterns of mule deer in an area affected by CWD, we did not address the effects of the CWD management program itself. Increased hunting pressure could have effects on movements and behavioural patterns of mule deer through increased disturbance during the hunting season and through changes in population structure or density. Future research should address this question by investigating mule deer movements and habitat use during the hunting season in areas of CWD management as compared to movements outside of the hunting season or in areas where herd reduction has not been implemented.

5.4 Conclusion

Although the true goal of this study was to determine factors that may affect the spread of chronic wasting disease by influencing deer movement and contact patterns, much of this research can be applied to the understanding and management of other diseases and parasites of deer in Saskatchewan. Mule deer and other cervids are highly valued in the province for economic, ecological and aesthetic reasons and efforts must be made to control the spread of chronic wasting disease within and outward from affected areas. Although a great deal of debate has surrounded the issue of long term population effects of CWD, researchers are beginning to

see evidence of deer population declines in areas of high CWD prevalence (Miller et al. 2008). Even without significant declines in deer and elk populations, the disease will result in damage to the hunting industry and major economic losses in affected provinces and states. Also, public health concerns and the unknown potential for CWD to move into caribou (*Rangifer tarandus*) populations of the north provide additional rationale for researchers and managers to continue their efforts in attempting to control the disease. The efforts currently underway can be aided by research programs such as this, which provide region-specific information on deer movement and behaviour that may be used to understand mechanisms of disease spread, develop predictive models, and improve the effectiveness of management strategies.

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